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**Uniparental incubation in a cool climate:  
behavioural adaptations in the Eurasian dotterel**

**S. Holt**

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## Abstract

Energetic constraint during reproduction may limit the number or quality of young that a parent can produce per breeding attempt or the parent's longevity or future productivity, ultimately constraining lifetime reproductive success. The Eurasian dotterel *Charadrius morinellus* experienced energetic constraint during the incubation period. Dotterel breed in the cold arctic-alpine zone and most breeding attempts are cared for by the male alone. The combination of a cold climate, giving high energetic costs of incubation and thermoregulation, and restricted foraging time due to uniparental incubation, resulted in non-adaptive mass loss and constrained investment of time and energy in incubation.

If the incubation period is potentially energetically constrained, then behavioural mechanisms that reduce energetic costs could increase the production of young. When more energetically constrained, dotterel reduced the energetic cost of incubation by scheduling trips in conditions when the unattended eggs would have cooled more slowly and by making fewer, but longer trips. When suffering severe energetic constraint, some dotterel neglected their eggs for many hours: dotterel embryos' high chilling tolerance may have been necessary for successful uniparental incubation in a cold and unpredictable environment. Dotterel selected nest sites that allowed them to build larger nests with larger linings. Larger, better insulated nests probably decreased heat loss from the eggs and sitting parents, so reducing energetic costs during incubation. Sitting dotterel oriented into the wind, which probably reduced the disruption of their plumage and minimised their energetic expenditure on thermoregulation. In cooler conditions, dotterel changed their nest defence strategy and used energetically cheaper but probably riskier responses to simulated predators.

Behaviours may be shaped under conflicting selective pressures and dotterel's management of their high energetic costs during the incubation period was constrained by egg-predation: dotterel's incubation scheduling appeared to be influenced by diurnal variation in the risk of predation and dotterel's nest defence behaviour traded-off energetic costs and the risk of predation.

I declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

This thesis presents data collected by myself over 2212h spent in the alpine study areas from 288 days during my PhD field seasons in 1996, 1997 and 1998. I also analyse some of Scottish Natural Heritage's dataset on dotterel biology collected between 1987 and 1999 by a team of fieldworkers, including myself (in Chapters 2, 7 and 8).

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## Chapter 1

### GENERAL INTRODUCTION

Individual animals are expected to behave in a way that maximises their fitness within the limitations of their biotic and abiotic environment (Darwin 1859; Krebs & Davies 1987). The fitness of an individual is its contribution to the gene pool of the following generations. Our best working measure of the fitness of an animal is generally its lifetime reproductive success (LRS, Grafen 1988; Clutton-Brock 1988a), which is the number of offspring an individual produces during its life or, less easily measured, its reproductive value, which also incorporates the effect of any changes in the size of the population (Daan & Tinbergen 1997). Since an individual cannot generally influence population changes (although it may respond to them, Clutton-Brock 1988a), LRS measures the element of an individual's fitness over which its behaviour may have most influence. For example, the frequency and intensity of reproductive effort may determine LRS (Clutton-Brock 1988b; Oring et al. 1991; Daan & Tinbergen 1997). Reproduction may reduce a parent's survival or future productivity if it makes high demands for time or energy, or if investment in reproduction increases the risk of being depredated or diseased (Pianka & Parker 1975; Partridge & Harvey 1985; Clutton-Brock 1988b; Partridge 1989; Daan & Tinbergen 1997). If reproduction is a significant energetic cost to the parents, energetic costs may constrain the number or quality of young produced per breeding attempt, the frequency of breeding attempts or the parents' longevity, ultimately constraining LRS (Martin 1987; Bryant 1988; Williams 1996; Daan & Tinbergen 1997; Monaghan & Nager 1997; Thomson et al. 1998). If the energetic costs of reproduction constrain LRS, then individuals whose behaviour reduces costs can produce more young and so have greater fitness. In this thesis I investigate whether a shorebird, the Eurasian dotterel *Charadrius morinellus*, experienced energetic constraint during the incubation period. I then asked how dotterel could behaviourally reduce their energetic costs, to lessen the degree of energetic constraint on LRS. Although I focus on the energetic costs of reproduction in dotterel, I also consider other potential costs, such as time and predation risk.

In birds, reproduction has three stages that may involve substantial energetic costs: egg production, incubation and chick rearing. Egg production may be an energetically costly stage of breeding that may limit the number, timing and quality of young that can be produced (Ricklefs 1974; Monaghan & Nager 1997): birds whose energy budgets are manipulated with supplementary food or by reducing thermostatic costs, change clutch and egg sizes, laying dates and laying intervals (reviewed in Monaghan & Nager 1997). Chick rearing is also frequently seen to be an energetically costly or energetically constrained stage of reproduction, especially in altricial birds, which spend much time and energy travelling to and from feeding sites while provisioning young (reviewed in Williams 1996; Monaghan & Nager 1997 & reviewed in Bryan & Bryant 1999). However, past studies have reached very different conclusions about the importance of the energetic costs of incubation (Kendeigh 1963; Walsberg 1983; Drent et al. 1985; Haftorn & Reinertsen 1985; Williams & Dwinell 1990b; Williams 1993; Slikamaki 1995; Williams 1996; Monaghan & Nager 1997; Thomson et al. 1998; Bryan & Bryant 1999). This is likely to reflect variation between study systems with different thermal environments (Walsberg 1983; Biebach 1984; Haftorn & Reinertsen 1985; Haftorn & Reinertsen 1990; Thomson et al. 1998), parental care systems (Williams 1996), clutch masses (Walsberg 1983; Biebach 1984; Haftorn & Reinertsen 1985; Haftorn & Reinertsen 1990; Thomson et al. 1998) and patterns of incubation (Vleck 1981a; Vleck 1981b; Webb & King 1983).

The energetic cost of incubation may be unlikely to constrain LRS in a species with biparental incubation or significant mate provisioning, large stores of body fat, a favourable nest microclimate, a small clutch mass and high rates of nest attendance (although energetic costs during the incubation period can be high even when most of these criteria are fulfilled, Thomson et al. 1998). Birds with large clutch masses relative to their body size are more likely to find incubation energetically costly as the energetic costs of incubation may increase with clutch mass (Biebach 1984; Haftorn & Reinertsen 1985; Coleman & Whittall 1988; Tøien 1989; Moreno & Sanz 1994). However, the most important determinants of whether the energetic cost of incubation is likely to constrain LRS are probably the parental care system and the environmental temperature. When a single parent carries out all incubation in a cold

nest microclimate, where the rate of heat loss from the eggs and parent will be high, then the energetic costs of incubation may potentially result in an energy shortfall (Williams 1996) and limit the number of young that can be produced (Kálás & Løfaldli 1987; Siikamaki 1995). A lone carer not only has to bear all the energetic costs of incubation itself but, unless it relies entirely on endogenous stores, its time in which to recoup these costs by foraging away from the nest is constrained by the time spent incubating (Williams 1996; Bryan & Bryant 1999). Also the parent will have to rewarm the eggs on its return after foraging (Williams 1996), further increasing its overall costs relative to constant incubation.

In some uniparental incubators the conflict between foraging and incubation time is resolved through provisioning by the non-incubating sex and the rate of provisioning correlates with measures likely to promote LRS (reviewed in Williams 1996). Other species with uniparental care solve this potential conflict by fuelling most or all of incubation using stored body reserves (e.g. Gabrielsen 1989; Reed et al. 1995). However, these 'capital' breeders are normally relatively large birds that, because of the difference in the allometric relationships of storage capacity and metabolic rate (Afton 1980; Croxall 1982; Walsberg 1983), are able to fuel themselves for longer using endogenous reserves. Smaller birds cannot store sufficient reserves for their entire incubation period and must leave the nest to feed (Williams 1996).

In summary, small, unprovisioned, uniparental incubators with large clutch masses and intermittent incubation in a cold climate are likely have high energetic costs of incubation. But how can we determine if the energetic costs of incubation are actually significant in terms of constraining LRS? Estimates of high energetic costs of incubation cannot alone demonstrate energetic constraint (Bryant & Tatner 1991), as the balance of the energy budget depends on energy inputs as well as energy outputs. An animal with very high energetic costs may not experience energetic constraint that limits LRS if it has high food intake or large body reserves to draw upon (Williams 1996). Collared flycatchers *Ficedula albicollis*, for example, can increase their energy expenditure on incubation with no apparent fitness costs (Moreno et al. 1991). Similarly, blue tit *Parus caeruleus* clutch sizes did not appear to be constrained by the high energetic cost of incubation, even though this cost increased with clutch size (Haftorn

& Reinertsen 1985). Conversely, when limited energy is available, even low energetic costs of incubation may result in energetic constraints that may limit LRS. For example, although common eider *Somateria mollissima* metabolic rate while incubating was lower than their resting metabolic rate (Gabrielsen 1989), eiders did not feed during the incubation period, so that clutch size appeared to be constrained by the net energy budget (Gabrielsen 1989; Erikstad & Tveraa 1995). Similarly, although incubation is not very energetically costly in common starlings *Sturnus vulgaris*, incubation scheduling is constrained by restricted foraging time (Drent et al. 1985).

Chick rearing or egg production are most frequently seen to be the energetic 'bottlenecks' of the reproductive cycle. However, even when this is the case, the energetic constraint experienced during incubation may influence LRS, since deficits in the energy budget at different stages of breeding may be cumulative: a reduction in body reserves through the incubation period may increase the degree of energetic constraint during a highly demanding chick-rearing phase (Moreno et al. 1991; Heaney & Monaghan 1996) or, when egg production is the most demanding stage, birds may have to hold back some body reserves to use during a less demanding incubation or chick-rearing period (Yom-Tov & Hilborn 1981; Gloutney & Clark 1993). For example, parents whose chick provisioning might be expected to be the bottleneck phase, that cared for experimentally enlarged clutches had lower breeding success than those that only had their chick rearing effort increased (Monaghan & Nager 1997).

If LRS is limited by the degree of energetic constraint experienced during incubation, then energy-saving behaviours could increase an individual's fitness. Thermogenesis for thermoregulation and incubation is probably the most important energetic cost for a uniparental incubator that spends most of its time on the nest in a cool climate (Bakken 1990; Piersma & Morrison 1994; Andreev 1999), so reducing heat loss from self and eggs will be an important way of saving energy. Rates of heat loss from the eggs can be reduced by characteristics of the nest and its contents (Drent 1975). This may simply take the form of reducing the surface area of the clutch that is exposed to cooling, either by a smaller clutch or tighter egg packing (Ricklefs 1974). The rate of heat loss from the clutch may be influenced



by the nest microclimate (Collias & Collias 1984). Selection of a nest site that is sheltered from the wind, exposed to insolation, remains dry and is warmer than surrounding areas may reduce the rate of heat loss from the eggs (Kondratiev 1982). A nest that is constructed of a large quantity of good insulating material could also reduce heat loss (Collias 1976; Thompson & Raveling 1987) and may allow parents to spend more time foraging (White & Kinney 1974). A uniparental incubator will spend most of its time sitting on the nest so that a nest microclimate that reduces heat loss from the eggs is also likely to reduce the parents' costs of thermoregulation (Calder 1973; Williams & Dwinell 1990a).

In species with intermittent incubation, a more subtle way of reducing heat loss from the eggs is through incubation scheduling (Vleck 1981a). Intermittent incubators must bear the cost of rewarming cool eggs after a trip away from the nest as well as the costs of steady-state incubation (the energy required to maintain eggs at stable temperature suitable for development once they are rewarmed). Exposed eggs follow a negative exponential cooling curve, so that they cool fastest at first (Ricklefs 1974). A large number of short trips will therefore mean greater rewarming costs for the parent than the same time spent on longer trips. For a given level of nest attendance (the proportion of time the clutch is incubated, Norton 1972) a parent can, then, vary the overall costs of incubation by varying trip length and frequency. The rate at which exposed eggs cool depends upon weather conditions and a parent may be able to reduce its rewarming costs by scheduling its trips in better weather conditions when the eggs cool more slowly (Purdue 1976; Cartar & Montgomerie 1985). Prey availability may also be greater when it is warmer (MacLean & Pitelka 1971).

When the eggs are unattended during feeding trips they may cool below a temperature suitable for development. Embryos appear to need to spend a certain amount of time at a suitable temperature to complete their development, so that more time being unattended may extend the incubation period, ultimately extending the time the parent is under energetic constraint (Vleck & Kenagy 1980). There may be other disadvantages to extension of the incubation period: the parent may further deplete its body reserves and have less time for further breeding attempts (Tombre & Erikstad 1996), while hatching success may reduce if

the probability of failure is a function of exposure time (Johnson 1979), and later hatched chicks may have reduced survival (e.g. Harris 1967; Perrins & McCleery 1989; references in Eichholz & Sedinger 1998; Siikamaki 1998). Most parents will not, anyway, have unlimited flexibility in scheduling incubation since embryos can be damaged or killed by relatively short exposure to the low or high temperatures they might experience while unattended (Webb 1987). In summary, a parent may use incubation scheduling to vary its overall energetic costs of incubation, although this will be constrained by the thermal sensitivity of the embryos and traded-off against any deleterious effects of extension of the incubation period.

A bird's behaviour during incubation cannot, however, be understood solely in terms of balancing the energy budget: behaviours may be shaped by conflicting selective pressures (Reznick 1985; Clutton-Brock 1988c; Daan & Tinbergen 1997). For example, attendance should be maximised to minimise the incubation period and the survival of the current offspring (Vleck & Kenagy 1980), but birds should also maintain their body condition to ensure their own survival to breed again and high nest attendance may compromise body condition (Bryant 1988; Erikstad et al. 1998). Maximising LRS means trading off these objectives (Afton & Paulus 1992). Similarly, avoidance of predation of self and eggs may also mean that incubation behaviours cannot be optimised solely in terms of energetic expenditure (Drent 1970; Norton 1972). In many tests of the overall hypothesis that birds should minimise energetic expenditure, trade-offs with other fitness considerations must be taken into account. As nest predation is such an important factor in reproductive success (Ricklefs 1969) this must often be considered as a constraint upon energy saving or to be traded off against energy saving (Skowron & Kern 1980; Marzluff 1988). For example, the risk of egg predation may increase as nest attendance declines (Drent 1970; Afton & Paulus 1992), increasing the pressure to maximise attendance. Predation of the eggs or chicks is the main cause of breeding failure in many bird species and protecting the clutch from predation is another potential energetic cost during the incubation period. The importance of this cost depends on the frequency of encounters with predators and the energetic cost of the type of nest defence used and, if the cost is potentially large, parents may be able to vary this cost through their defence strategy.

This study uses the adaptive approach to investigate the behaviours the Eurasian dotterel uses during incubation to maximise its LRS. If parents experience energetic constraint during the incubation period, selection will favour individuals with behavioural adaptations that reduce costs, potentially increasing their production of independent young. Dotterel fit many of the criteria for a species that is likely to have high energetic costs during incubation that may limit LRS: dotterel might then be expected to exhibit energy saving behaviours.

Firstly, the dotterel's cool, wet and windy, arctic-alpine breeding environment (Cramp & Simmons 1983; McClatchey 1996) probably gives them relatively high energetic costs of incubation and thermoregulation (Piersma & Morrison 1994; Andreev 1999). Like most shorebirds, dotterel nest on the ground (Cramp & Simmons 1983; del Hoyo et al. 1996) and the rate of conductive heat loss from the eggs to the cold ground may be high (Andreev 1999). The same harsh environment may also result in periods of reduced food availability, for example during periods of high snow cover (Cartar & Montgomerie 1985; Owens 1991) or during colder weather (MacLean & Pitelka 1971).

Secondly, dotterel have a three egg clutch that averages 43% of their body mass (D.P. Whitfield unpublished data) and is relatively loosely packed compared with the more common four egg clutches of other temperate and arctic shorebirds. This loose egg packing may increase the effective surface area over which heat is lost, increasing the energetic cost of incubation (Norton 1970 cited in Ricklefs 1974). Norton's (1970) estimates of higher cooling rates in three egg clutches than four egg clutches were based on dunlin *Calidris alpina* eggs that are shaped for optimal packing in a typically four egg clutch. Although dotterel eggs are shaped for better packing within a three egg clutch (the optimal packing for a three egg clutch is biconical compared with pointed eggs for a four egg clutch, Barta & Székely 1997), their packing appears loose compared to shorebirds with typically four egg clutches, so that the relative rate of heat loss is probably high.

Thirdly, and perhaps most importantly, most breeding attempts are uniparental. The male parent alone has to bear all the higher energetic costs of intermittent incubation and has a relatively limited foraging time in which to recoup these costs.

I attempt to determine, in two ways, whether the potentially high energetic costs and limited foraging time of uniparental dotterel result in energetic constraint likely to limit the LRS: firstly by investigating whether incubating dotterel depleted their body reserves below their optimal level and, secondly, by exploring whether incubation scheduling was energetically constrained.

I investigate whether dotterel are energetically constrained during the incubation period by testing whether dotterel showed non-adaptive mass loss as a consequence of using body reserves. Depletion of body reserves may indicate energetic constraint and individuals with smaller masses relative to their structural size have often been assumed to be under greater energetic stress, having been compelled to use more body reserves to supplement their energy budgets (reviewed in Moreno 1989b). When parents are compelled to utilise endogenous reserves so that they fall below their desired level, this may have fitness consequences for both the parent and young (reviewed in Bryant 1988; Hepp et al. 1990; reviewed in Arnold et al. 1995; Blums et al. 1997). However, in the light of the benefits of lower wing loadings for flight performance (Pennycuik 1989; Veasey et al. 1998), reduced body reserves are no longer thought to always indicate energetic constraint (Witter & Cuthill 1993). To prove that mass loss is a consequence of energetic constraint we must show that birds increase in mass when the putative energetic constraint is lifted (Merkle & Barclay 1996).

I also investigate whether dotterel are energetically constrained during the incubation period by testing whether nest attendance varied with the factors that would influence their energy budget. Energetic constraint during the incubation period can be demonstrated by showing that parents are able to spend more time incubating when the cost of incubation is experimentally reduced (Bryan & Bryant 1999; Reid et al. 1999) or naturally lower (Norton

1973) or when their energetic inputs were experimentally increased with supplementary food (Erikstad 1986; Smith et al. 1989; Moreno 1989a) or, conversely, that attendance declines with naturally or experimentally increased costs (Kálás & Løfaldli 1987).

Although most dotterel nests have male uniparental care, 17% had biparental care in this study (a relatively high proportion for Scotland, D.P. Whitfield unpublished). Biparental males are probably less energetically constrained than uniparental males as, by sharing incubation duties, they have reduced costs of incubation and, probably more importantly, they have greater off-duty time to forage. Variation in the parental care of dotterel, and the consequent variation in the degree of energetic constraint experienced, provided a useful tool for investigating adaptations to the degree of energetic constraint experienced during incubation.

If dotterel experience energetic constraint during incubation then behaviours that reduce their energetic expenditure could increase their fitness. Lastly, I test the hypothesis that dotterel behaviourally reduce their level of energetic constraint by reducing energetic costs through their incubation scheduling, nest microclimate selection and nest defence behaviour against predators.

## References

- Afton, A.D. 1980. Factors affecting incubation rhythms of Northern Shovelers. The Condor, 82, 132-137.
- Afton, A.D. & Paulus, S.L. 1992. Incubation and brood care. In: Ecology and management of breeding waterfowl (Ed. by B.D. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, & G.L. Krapu), pp. 62-108. Minneapolis: University of Minnesota Press.
- Andreev, A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich, 70, 13-22.

- Arnold, T.W., Anderson, M.G., Emery, R.B., Sorenson, M.D. & de Sobrino, C.N. 1995. The effects of late-incubation body-mass on reproductive success and survival of Canvasbacks and Redheads. The Condor , 97, 953-962.
- Bakken, G.S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk , 107, 587-594.
- Barta, Z. & Székely, T. 1997. The optimal shape of avian eggs. Functional Ecology , 11, 656-662.
- Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating Starlings (*Sturnus vulgaris*). Physiological Zoology , 57, 26-31.
- Blums, P., Mednis, A. & Clark, R.G. 1997. Effect of incubation body mass on reproductive success and survival of two European diving ducks: a test of the nutrient limitation hypothesis. The Condor , 99, 916-925.
- Bryan, S.M. & Bryant, D.M. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in Great Tits, *Parus major*. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 266, 157-162.
- Bryant, D.M. 1988. Energy expenditure and body mass changes as measures of reproductive cost in birds. Functional Ecology , 2, 23-34.
- Bryant, D.M. & Tatner, P. 1991. Intraspecific variation in avian energy expenditure: correlates and constraints. Ibis , 133, 236-245.
- Calder, W.A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comparative Biochemistry and Physiology , 46, 291-300.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour , 95, 261-289.
- Clutton-Brock, T.H. 1988a. Reproductive success. In: Reproductive success: studies of individual variation in contrasting breeding systems (Ed. by T.H. Clutton-Brock), pp. 472-485. Chicago: Chicago University Press.
- Clutton-Brock, T.H. 1988b. Reproductive success: studies of individual variation in contrasting breeding systems. Chicago: Chicago University Press.

- Clutton-Brock, T.H. 1988c. Introduction. In: Reproductive success: studies of individual variation in contrasting breeding systems (Ed. by T.H. Clutton-Brock), pp. 1-10. Chicago: University of Chicago.
- Coleman, R.M. & Whittall, R.D. 1988. Clutch size and the cost of incubation in the Bengalese Finch (*Lonchura striata* var. *domestica*). Behavioural Ecology and Sociobiology, 23, 367-372.
- Collias, N.E. & Collias, E.C. 1976. External construction by animals. Stroudsburg, Pennsylvania: Dowden, Hutchinson & Ross, Inc.
- Collias, N.E. & Collias, E.C. 1984. Nest building and bird behaviour. Cambridge: Harvard University Press.
- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic: Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Croxall, J.P. 1982. Energy cost of incubation and moult in petrels and penguins. Journal of Animal Ecology, 51, 177-194.
- Daan, S. & Tinbergen, J.M. 1997. Adaptation of life histories. In: Behavioural ecology: an evolutionary approach (Ed. by J.R. Krebs & N.B. Davies), pp. 311-333. Oxford: Blackwell Scientific.
- Darwin, C. 1859. The origin of the species. London: Murray.
- del Hoyo, J., Elliott, A. & Sargatal, J. 1996. Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks. Barcelona: Lynx Edicions.
- Drent, R.H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Supplement, 17, 1-132.
- Drent, R.H. 1975. Incubation. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 333-420. New York: Academic Press.
- Drent, R.H., Tinbergen, J.M. & Biebach, H. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands Journal of Zoology, 35, 103-123.
- Eichholz, M.W. & Sedinger, J.S. 1998. Factors affecting duration of incubation in Black Brant. The Condor, 100, 164-168.

- Erikstad,K.E. 1986. Relationship between weather, body condition and incubation rhythm in Willow Grouse. Fauna norvegica Ser. C Cinclus , 9, 7-12.
- Erikstad,K.E., Fauchald,P., Tveraa,T. & Steen,H. 1998. On the cost of reproduction in long-lived birds: The Influence of environmental variability. Ecology , 79, 1781-1788.
- Erikstad,K.E. & Tveraa,T. 1995. Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*. Oecologia , 103, 270-274.
- Gabrielsen,G.W. 1989. Energy saving in incubating birds. In: Physiology of cold adaptation in birds (Ed. by C.Bech & R.E.Reinertsen), pp. 325-328. New York: Plenum Press.
- Gloutney,M.L. & Clark,R.G. 1993. The significance of body mass to female dabbling ducks during late incubation. The Condor , 93, 811-816.
- Grafen,A. 1988. On the uses of data on lifetime reproductive success. In: Reproductive success: studies of individual variation in contrasting breeding systems (Ed. by T.H.Clutton-Brock), pp. 454-471. Chicago: Chicago University Press.
- Haftorn,S. & Reinertsen,R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit. Auk , 102, 470-478.
- Haftorn,S. & Reinertsen,R.E. 1990. Thermoregulatory and behavioral responses during incubation of free-living Pied Flycatchers *Ficedula hypoleuca*. Ornis Scandinavica , 21, 255-264.
- Harris,M.P. 1967. The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. Ibis , 109, 180-193.
- Heaney,V. & Monaghan,P. 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 263, 1719-1724.
- Hepp,G.R., Kennamer,R.A. & Harvey,W.F. 1990. Incubation as a reproductive cost in Wood Ducks. Auk , 107, 756-764.
- Johnson,D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk , 96, 651-661.
- Kálás,J.A. & Løfaldli,L. 1987. Clutch size in the Dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? Ornis Scandinavica , 18, 316-319.



- Kendeigh, S.C. 1963. Thermodynamics of incubation in the house wren, *Troglodytes aedon*.  
In: Proceedings of the XIII International Ornithological Congress pp. 884-904.
- Kondratiev, A.J. 1982. Biology of waders in the tundras of the north-east of Asia. Academy of Sciences of the USSR: Nauka, Moscow
- Krebs, J.R. & Davies, N.B. 1987. An introduction to behavioural ecology. 2nd edn.
- MacLean, S.F.Jr. & Pitelka, F.A. 1971. Seasonal patterns of abundance in tundra arthropods near Barrow, Alaska. Arctic, 24, 19-40.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics, 18, 453-487.
- Marzluff, J.M. 1988. Do Pinyon Jays alter nest placement based on prior experience. Animal Behaviour, 36, 1-10.
- McClatchey, J. 1996. Spatial and altitudinal gradients of climate in the Cairngorms- observations from climatological and automatic weather stations. Botanical Journal of Scotland, 48, 31-49.
- Merkle, M.S. & Barclay, R.M.R. 1996. Body mass variation in breeding Mountain Bluebirds *Sialia currucoides*: evidence of stress or adaptation to flight? Journal of Animal Ecology, 65, 401-413.
- Monaghan, P. & Nager, R.G. 1997. Why don't birds lay more eggs? Trends In Ecology & Evolution, 12, 270-274.
- Moreno, J. 1989a. Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe*. Ardea, 77, 107-115.
- Moreno, J. 1989b. Strategies of mass change in breeding birds. Biological Journal of the Linnean Society, 37, 297-310.
- Moreno, J., Gustafsson, L., Carson, A. & Pärt, T. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. Ibis, 133, 186-193.
- Moreno, J. & Sanz, J.J. 1994. The relationship between the energy-expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. Journal of Avian Biology, 25, 125-130.
- Norton, D.W. 1972. Incubation schedules of four species of Calidrine sandpipers at Barrow, Alaska. The Condor, 74, 164-176.

- Norton,D.W. 1973. Ecological energetics of Calidrine sandpipers breeding in northern Alaska. PhD thesis, University of Alaska, Fairbanks.
- Oring,L.W., Colwell,M.A. & Reed,J.M. 1991. Lifetime reproductive success in the Spotted Sandpiper (*Actitis macularia*): sex differences and variance components. Behavioural Ecology and Sociobiology , 28, 425-432.
- Owens,I.P.F. 1991. Sexual selection in the sex-role reversed dotterel, *Charadrius morinellus*. PhD thesis, University of Leicester.
- Partridge,L. 1989. Lifetime reproductive success and life-history evolution. In: Lifetime reproduction in birds (Ed. by I.Newton), pp. 421-440. London: Academic Press.
- Partridge,L. & Harvey,P.H. 1985. Costs of reproduction. Nature , 316, 20
- Pennycuick,C.J. 1989. Bird flight performance: A practical calculation manual. Oxford: Oxford University Press.
- Perrins,C.M. & McCleery,R. 1989. Laying dates and clutch size in the Great Tit. Wilson Bulletin , 101, 236-253.
- Pianka,E.R. & Parker,W.S. 1975. Age-specific reproductive tactics. American Naturalist , 109, 453-464.
- Piersma,T. & Morrison,R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.
- Purdue,J.R. 1976. Thermal environment of the nest and related parental behaviour in snowy plovers, *Charadrius alexandrinus*. The Condor , 78, 180-1851.
- Reed,A., Hughes,R.J. & Gauthier,G. 1995. Incubation behaviour and body mass in Greater Snow Geese. The Condor , 97, 993-1001.
- Reid,J.M., Monaghan,P. & Ruxton,G.D. 1999. The effect of cooling rate on starling, *Sturnus vulgaris*, incubation strategy. Animal Behaviour , 58, 1161-1167.
- Reznick,D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos , 44, 257-267.
- Ricklefs,R.E. 1969. An analysis of nesting mortality in birds. Smiths. Cont. Zool. 9, 1-48.
- Ricklefs,R.E. 1974. Energetics of reproduction in birds. In: Avian energetics (Ed. by R.A.J.Paynter), pp. 152-297. Nuttall Ornithological Club.

- Siikamäki, P. 1995. Are large clutches costly to incubate? - the case of the Pied Flycatcher. Journal of Avian Biology , 26, 76-80.
- Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. Ecology , 79, 1789-1796.
- Skowron, C. & Kern, M. 1980. The insulation in nests of selected North American songbirds. Auk , 97, 816-824.
- Smith, H.G., Källander, H., Hultman, J. & Sanzén, B. 1989. Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. Behavioural Ecology and Sociobiology , 24, 417-420.
- Thompson, S.C. & Raveling, D.G. 1987. Incubation behaviour of Emperor Geese compared to other Geese: interactions of predation, body size and energetics. Auk , 104, 707-716.
- Thomson, D.L., Monaghan, P. & Furness, R.W. 1998. The demands of incubation and avian clutch size. Biological Reviews , 73, 293-304.
- Tombre, I.M. & Erikstad, K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Tøien, Ø. 1989. Effect of clutch size on efficiency of heat transfer to cold eggs in bantam hens. In: Physiology of cold adaptation in birds (Ed. by C. Bech & R.E. Reinertsen), pp. 305-313. New York: Plenum Press.
- Veasey, J.S., Metcalfe, N.B. & Houston, D.C. 1998. A reassessment of the effect of body mass upon flight speed and predation risk in birds. Animal Behaviour , 56, 883-889.
- Vleck, C.M. 1981a. Energetic cost of incubation in the Zebra Finch. The Condor , 83, 229-237.
- Vleck, C.M. 1981b. Hummingbird incubation: female attentiveness and egg temperature. Oecologia , 51, 199-205.
- Vleck, C.M. & Kenagy, G.J. 1980. Embryonic metabolism of the Fork-tailed Storm Petrel: physiological patterns during prolonged and interrupted incubation. Physiological Zoology , 53, 32-42.
- Walsberg, G.E. 1983. Avian ecological energetics. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 161-220. New York: Academic Press.
- Webb, D.R. 1987. Thermal tolerance of avian embryos: A review. The Condor , 89, 874-898.

- Webb,D.R. & King,J.R. 1983. An analysis of the heat budgets of the eggs and nest of the White-crowned Sparrow, *Zonotrichia leucophrys*, in relation to parental attentiveness. Physiological Zoology , 56, 493-505.
- White,F.N. & Kinney,J.L. 1974. Avian incubation. Science , 186, 107-115.
- Williams,J.B. 1993. Energetics of incubation in free-living Orange-breasted Sunbirds in South Africa. The Condor , 95, 115-126.
- Williams,J.B. 1996. Energetics of avian incubation. In: Avian energetics and nutritional ecology (Ed. by C.Carey), pp. 375-415. New York: Chapman & Hall.
- Williams,J.B. & DwinneI,B. 1990a. Field metabolism of free-living female Savannah Sparrows during incubation: a study using doubly labelled water. Physiological Zoology , 63, 353-372.
- Williams,J.B. & DwinneI,B. 1990b. Incubation energetics of female Savannah Sparrows. Physiological Zoology , 63, 353-372.
- Witter,M.S. & Cuthill,I.C. 1993. The ecological costs of avian fat storage. Philosophical Transactions of the Royal Society of London, series B , 340, 73-92.
- Yom-Tov,Y. & Hilborn,R. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia , 48, 234-243.

## Chapter 2

### MASS LOSS IN INCUBATING EURASIAN DOTTEREL: ADAPTATION OR CONSTRAINT?

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## Mass loss in incubating Eurasian dotterel: adaptation or constraint?

Sue Holt, D. Philip Whitfield, Keith Duncan, Stuart Rae and Rik D. Smith

Holt, S., Whitfield, D. P., Duncan, K., Rae, S. and Smith, R. D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? – J. Avian Biol. 33: 219–224.

Body mass loss is frequently observed in breeding birds: whether this is an adaptive response to a change in the relative value of body stores and locomotion performance or a consequence of energetic constraint is still in debate. The male alone cares for most nests of the Eurasian dotterel *Charadrius morinellus*, although females assist at a proportion of nests. Energetic costs are probably high in the dotterel's arctic-alpine environment and uniparental care restricts the foraging time available to meet these costs, so that incubating dotterel may have to fuel themselves partly using body stores. Nesting male dotterel lost 7.8% of their mass through the incubation period but were 6.8% heavier during periods of high food abundance. Males that were assisted in incubation by a female were 6.7% heavier than uniparental males. We conclude that, since dotterel were heavier when energetic constraints were lifted, mass loss through incubation was principally a consequence of energetic constraint, rather than adaptive mass optimisation.

*S. Holt (correspondence), Institute of Biological Sciences, University of Stirling, Stirling, UK, FK9 4LA. Present address: 34 Acre End Street, Eynsham, Oxfordshire, UK, OX29 4PA. E-mail: sue@holicress.freeserve.co.uk. D. P. Whitfield, K. Duncan, S. Rae and R. D. Smith, Scottish Natural Heritage, 2 Anderson Place, Edinburgh, UK, EH16 5NP.*

Early studies on body mass changes in birds tended to assume that mass loss was generally a non-adaptive consequence of a shortfall in the energy budget, and that heavier birds were in good condition or were individuals of better quality (reviewed in Moreno 1989a and Williams 1996). However, with increased understanding of the relationship between locomotion costs and mass, and of mass-dependent predation risk, birds are now thought to be balancing locomotory performance against the benefits of body stores, so that heavier individuals may even be interpreted to be of poorer quality, or face more unpredictable food resources or energetic costs (Witter and Cuthill 1993). The optimal level of body stores for an individual bird at any time balances conflicting costs and benefits (Witter and Cuthill 1993). Greater stores may fuel a bird through periods of increased energetic costs or decreased food availability (Merkle and Barclay 1996) but will increase mass and may reduce an individual's flight performance (Veasey et al. 1998), possibly increasing its vulnerability to predators, and make flight or terrestrial

locomotion more energetically costly (Witter and Cuthill 1993, Bruinzeel and Piersma 1998). The relative importance of the costs and benefits of carrying stores may vary with climatic conditions, predator abundance, food availability, migration, season or stage of breeding (Witter and Cuthill 1993). However, if food intake is low and energetic demands are high, individuals may not be able to achieve their optimal masses. Mass loss is often observed in breeding birds (reviews in Norberg 1981 and Moreno 1989a) and we have to determine whether this is individual mass optimisation (i.e. 'adaptive') or a consequence of energetic constraint, when energetic costs are high or food intake is restricted (Witter and Cuthill 1993, Williams 1996). The coincidence of mass loss with a period of high energetic demand is not sufficient to demonstrate energetic constraint as individuals may use body stores accumulated for that purpose, without deviating from their optimal mass trajectory. To determine whether mass loss is adaptive or is a consequence of energetic constraint we must measure whether less mass is lost when the puta-

tive energetic constraint is lifted. A number of studies that used supplementary food to ensure that energetic constraints were not operating found that patterns of mass loss were generally unchanged, concluding that mass loss during breeding was adaptive (Moreno 1989b, Merkle and Barclay 1996, Cavitt and Thompson 1997, Slagsvold and Johansen 1999). In contrast, Cucco and Malacarne (1997) found that supplemented birds were heavier, suggesting mass loss was due to energetic constraint. In this paper we investigate the patterns of mass change in breeding Eurasian dotterel *Charadrius morinellus* in the presence and absence of foraging constraints, to determine whether mass loss is adaptive or a consequence of energetic constraint.

The Eurasian dotterel is a shorebird that nests on the ground in the cool arctic-alpine zone, where the energetic costs of thermoregulation and incubation are likely to be high (Piersma and Morrison 1994, Andreev 1999). As most nests are cared for by the male alone (Cramp and Simmons 1983), the parent has limited foraging time in which to recoup costs (Kálás 1986). Because of high energetic costs, a variable climate and restricted foraging time, incubating dotterel may be particularly susceptible to periods of energetic shortfall when mass loss might result from constraint. Mass loss during incubation has been demonstrated in dotterel (Kálás and Byrkjedal 1984, Pulliainen and Saari 1992) and mass loss may increase with increased incubation effort (Kálás and Lofaldi 1987). If this is a consequence of energetic constraint, rather than adaptive, we would predict that dotterel have higher masses for their stage in incubation when constraints on their energy budgets are lifted through increased food availability. In this study we investigated the pattern of mass loss in dotterel in Scotland during the incubation period. We determined whether mass loss was a consequence of energetic constraint by testing whether male dotterel were heavier during periods of high food abundance or at biparental nests, at which foraging time was less restricted.

## Methods

We captured 216 nesting male dotterel using walk-in nest traps or single-shelf mist nets on 10 low- and mid-alpine sites in the Highlands of Scotland between 1987–1993 and 1996–1999. Sites were 'islands' of alpine habitat on the tops of hills, separated from each other by at least 1 km of lower altitude habitats not used by breeding dotterel. We do not give site names or locations as dotterel are vulnerable to egg-collectors. We measured mass to 0.5 g using spring balances and wing length (maximal chord) to 0.5 mm on a stopped wing ruler. We sexed dotterel in the field using plumage characters. Body mass varies with structural size as well

as with body stores so, to obtain a measure of an individual's body stores, we controlled for structural size using wing length. Body mass may not be linearly related to wing length. To determine the function relating the two, we regressed the log of body mass of nesting dotterel against the log of wing length. As the coefficient for logged wing length was not significantly different from one ( $\log(\text{mass}) = 0.903 \pm 0.427\log(\text{wing}) + c$ ) we assume a linear relationship in the following analyses and predict mass from wing length using these regression coefficients (linear regression:  $F_{1,214} = 18.001$ ,  $P < 0.001$ ,  $R_{\text{adj}}^2 = 0.073$ ,  $\text{mass} = 8.519 + 0.685\text{wing length}$ ).

We used the availability of the crane fly *Tipula montana* as a measure of foraging constraint. Adult *T. montana* are relatively large and slow moving and very abundant (up to 2 counted per m<sup>2</sup>) during the typically 3-week emergence period (range 1–5 weeks, D. P. Whitfield unpubl.). When available, either as adults or as large, second-year, pre-emergence larvae that live close to the ground surface (D. Horsfield pers. comm.), *T. montana* forms an important part of dotterel's diet (e.g., in an emergence year on site B, 72% of the prey items in the faeces of male dotterel caring for chicks were *Tipula*, Galbraith et al. 1993). That *T. montana* is important for dotterel is clear from findings such as that they spend more time off the nest foraging when *T. montana* is not available (own unpubl.). In the alpine zone, the adult *T. montana* emerges in the second year after being laid as an egg (D. P. Whitfield unpubl.). The pattern of emergence of *T. montana* varied between sites and years. For example, between 1987 and 1999, site B had emergences only in even-numbered years, whereas *T. montana* generally emerged in odd-numbered years at site D and there was an emergence at site A every year (D. P. Whitfield unpubl.).

We measured the abundance of adult *T. montana* from transects. Approximately every three days, the observer slowly walked five to ten 10 m transects at random locations in areas used by feeding dotterel and counted the number of adult *T. montana* seen in a 2 m band centred along each transect. Additionally, the number of adult *T. montana* trapped in water baths was counted approximately every three days for some years at sites A, B and C; in 1990, water baths provided the only abundance data for site E (two baths were placed in a typical stand of each major plant community). At site A the total number of adult *T. montana* seen per day was also estimated and recorded on a log scale (0, 1–10, 11–100, 101–1000, > 1000). An emergence was taken to start and finish when the first and last adult *T. montana* was recorded by any of these methods. When an adult emergence was observed the earlier availability of pre-emergence larvae could be assumed from their life-cycle. For site-years in which there was no *T. montana* emergence, the start and finish of the notional emergence periods were taken to equal the mean start

and finish dates for years in which there was an emergence on that site. The availability of *T. montana* was not recorded for all sites and years, but was known for 196 captured nesting dotterel from six sites, for between one and ten years per site.

If we saw a female incubating a clutch after the day it was completed we classified the nest as having biparental care (female uniparental care has not been recorded: Cramp and Simmons 1983, D. P. Whitfield unpubl.). Of 196 nesting dotterel 93.9% were classified as incubating alone and the remaining 6.1% as biparental. By chance, we may never have visited some biparental nests while the female was sitting and so would have incorrectly classified them as uniparental. We estimate that only 1.5% of nests classified as uniparental were biparental, assuming that the probability of detecting a female at a biparental nest is the cumulative distribution function of the binomial distribution, where the probability of seeing a female on a single nest visit equals 0.35 (a rough estimate of the proportion of incubation contributed by females at biparental nests, D. P. Whitfield unpubl.).

An advantage of studying mass loss in the sex-role reversed male dotterel is that atrophy of the reproduc-

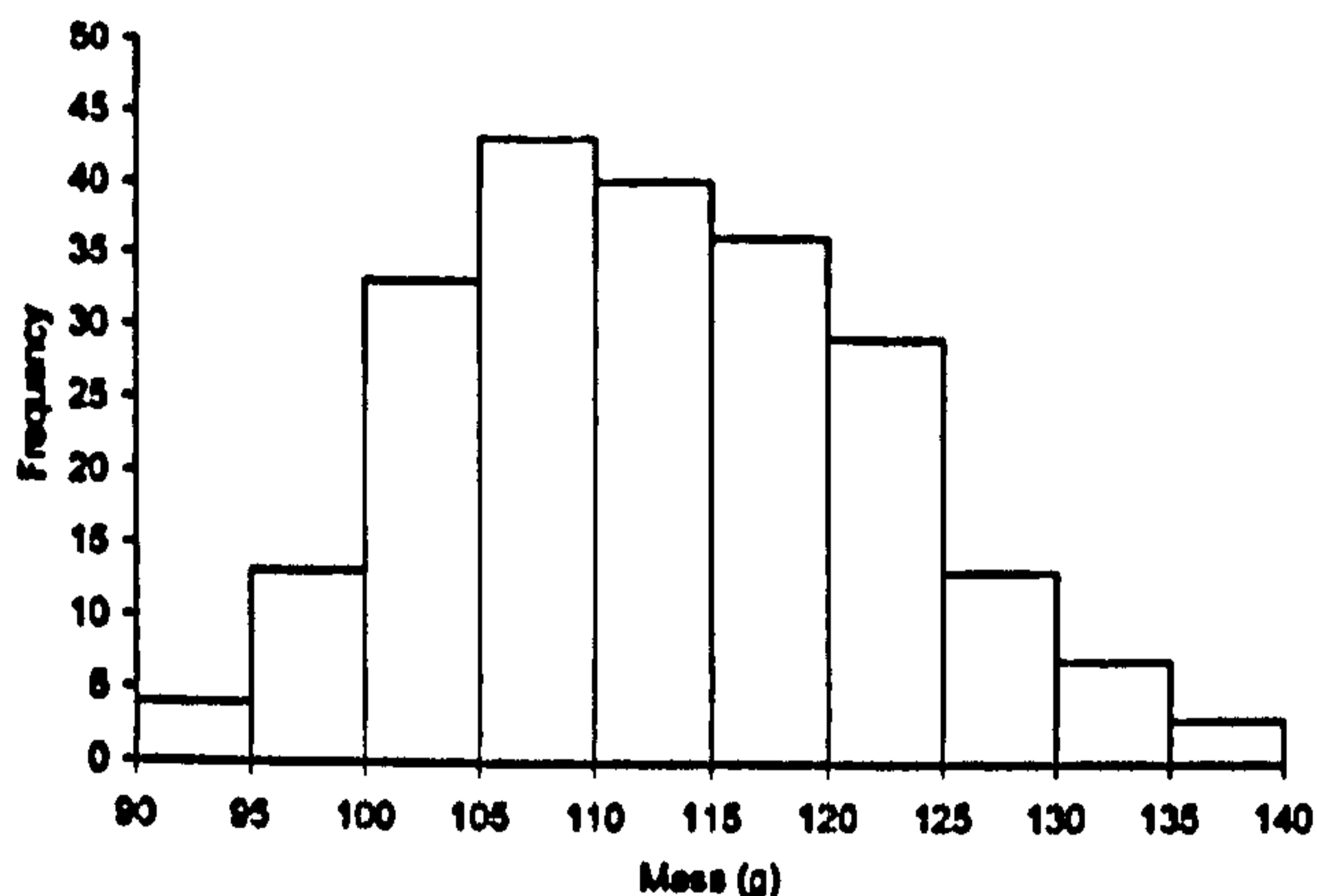


Fig. 1. Variation in the body mass of nesting male dotterel.

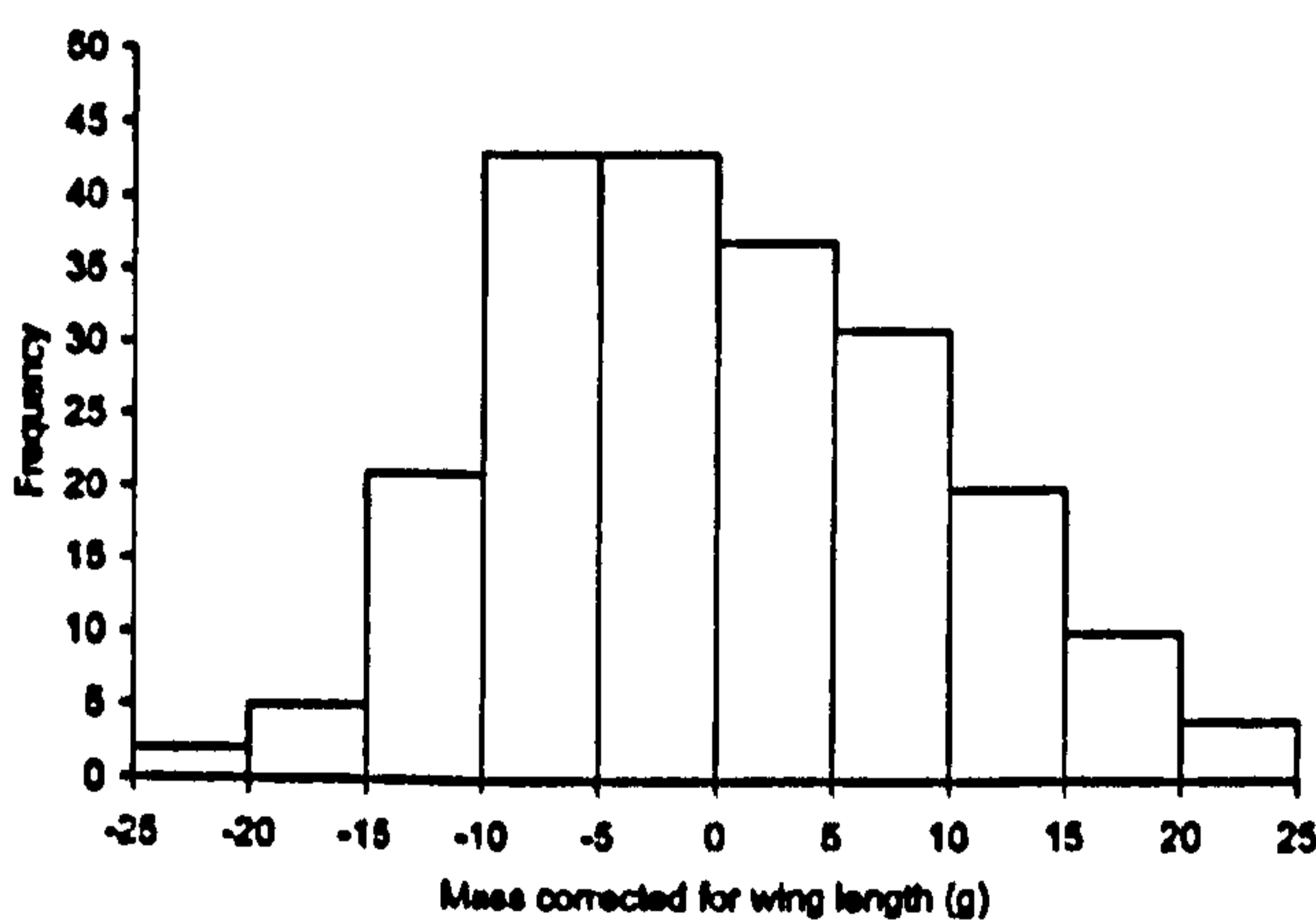


Fig. 2. Variation in the body stores of nesting male dotterel: mass corrected for wing length.

tive organs is unlikely to influence mass change as it may in females of some species (Ricklefs and Hussell 1984). Male reproductive organs may initially weigh less than those of females (Ricklefs 1974) and since male dotterel can pair with a new female within a day of losing a clutch and can initiate a new clutch within six days, there may be little atrophy (D. P. Whitfield unpubl.).

Nests were found by random searching or observing parental activity and were checked approximately every three days. The date that a clutch was initiated (first egg date) was observed, estimated from hatch date (assuming a 28-day period from first egg laid to last chick hatched; Cramp and Simmons 1983, D. P. Whitfield unpubl.), or estimated from an equation relating egg density to days until hatch (derived from measurements of clutches of known hatch date, D. P. Whitfield unpubl.).

Statistical tests were carried out using SPSS (Norusis 1990) and we state means  $\pm$  95% c.i. We give two-tailed probabilities and we include only one datum per individual to avoid pseudoreplication.

## Results

There was much variation in the body mass of incubating dotterel (mean:  $113.5 \pm 1.5$  g, range: 92.0 to 139.0 g, Fig. 1) and in mass corrected for wing length, which provides a measure of body stores (range: -22.0 to 24.5 g, Fig. 2). The lightest bird, trapped with chicks when it had a residual mass of -35.5 g, only 68% of its predicted mass, may represent the lower viable limit of body stores since this individual could barely fly at the time of capture, although it later flew normally after deserting its brood.

We used general linear modelling (GLM) to test whether mass varied through the incubation period (days since first egg date), with parental care (uniparental or biparental) and *Tipula montana* availability as main effects and included terms for site, wing length and first egg date to control for confounding effects (Table 1). The high abundance of adult *T. montana* during emergences seems likely to increase dotterel's food availability but we could not be sure whether the large, pre-emergence larvae would similarly improve food availability. Terms for whether adult *T. montana* were available and for whether adult or pre-emergence larval *T. montana* were available both significantly accounted for variation in mass when each was included in a separate model similar to that in Table 1. However, when both were included in the same model the term for the availability of adult or pre-emergence larval *T. montana* remained significant ( $F_{1,184} = 8.064$ ,  $P = 0.005$ ) whereas the term for the availability of just adult *T. montana* became non-significant ( $F_{1,184} = 1.506$ ,  $P =$



Table 1. GLM of the factors affecting the mass of incubating male dotterel.

Source	df	F	P	Partial R <sup>2</sup>
Intercept	1,185.7	0.43	0.515	
Parental care	1,185	6.23	0.013	0.033
Site	5,185	3.02	0.012	0.076
Days since first egg date	1,185	11.42	<0.001	0.058
Availability of <i>Tipula montana</i> adults or pre-emergence larvae	1,185	21.78	<0.001	0.105
First egg date	1,185	0.00	0.976	
Wing length	1,185	16.04	<0.001	0.080

0.221). Hence we used the availability of adult or pre-emergence larval *T. montana* as a measure of food availability in the GLM (Table 1 and Fig. 3). Parental care and *T. montana* availability were entered as fixed factors, site as a random factor and days since first egg date, wing length and first egg date as covariates. Dotterel lost an estimated 9.4 g or 7.8% (calculated by substituting mean values for all other terms in the GLM) of their initial mass during the mean 28-day period from clutch initiation to hatch. When adult or pre-emergence larvae of *T. montana* were available, dotterel were an estimated 7.6 g or 6.8% heavier when trapped. Males at biparental nests were 7.8 g or 6.7% heavier when trapped than those incubating alone. In addition, the only male that was trapped at both a biparental and uniparental nests had a residual mass of 17.0 g at the biparental nest and a residual mass of only -3.0 g at a uniparental nest in the following year (mass corrected for all terms in the GLM except parental care).

Male age was not included in the GLM as it was known for too few individuals to give an adequate sample size but, if body stores vary with age, this could have confounded our analysis. However, there was no significant difference between individuals' masses, corrected for terms in the previous model, when they were younger and when they were older (paired t-test:  $T_{11} = 0.591$ ,  $P = 0.566$ , Residual mass was  $1.5 \pm 4.5$  g less when dotterel were older by a median of 1.5 years).

## Discussion

Dotterel lost a mean of 7.8% of their mass through the incubation period but, after accounting for this, were 6.8% heavier during periods of high food abundance. Males at biparental nests were 6.7% heavier than uniparental males. As dotterel had higher residual masses when energetic constraints were lessened or absent, we conclude that they lost mass through the incubation

period as a consequence of energetic constraint rather than mass optimisation. Dotterel's optimal masses are likely to balance their requirements for buffer stores to cover energy-budget deficits against the costs of carrying additional mass (Witter and Cuthill 1993). We do not know how the costs of additional mass may vary in dotterel but the benefits of a buffer of body stores appear to be high for biparental shorebirds in cold Arctic climates (Soloviev and Tomkovich 1997) and are likely to be even more important in a uniparental incubator.

In this study, dotterel lost an estimated mean 7.8% of their initial mass through the incubation period, similar to the mass change in a Norwegian study but only one third of the mass loss recorded in Finland (Kålås and Byrkjedal 1984, Pulliainen and Saari 1992). The difference in mass loss between the studies may reflect differences in environmental conditions and the severity of the energetic shortfall dotterel experienced (Harvey 1971, Schamel and Tracy 1987, Gaston and Jones 1989, Harvey et al. 1989, Pulliainen and Saari 1992, Wendeln and Becker 1996). An individual or population may not always fit either of the adaptive or energetic constraint paradigms of mass loss as energetic constraints may only operate under some conditions. For example, in poor conditions mass stores may be depleted below the optimal level while, in good conditions, stores may be used to fuel a demanding period without deviating from an optimal mass trajectory or, alternatively, shed when no longer required (Merkle and Barclay 1996).

The high energetic costs of incubation in a cool climate may make it difficult for a uniparental incuba-

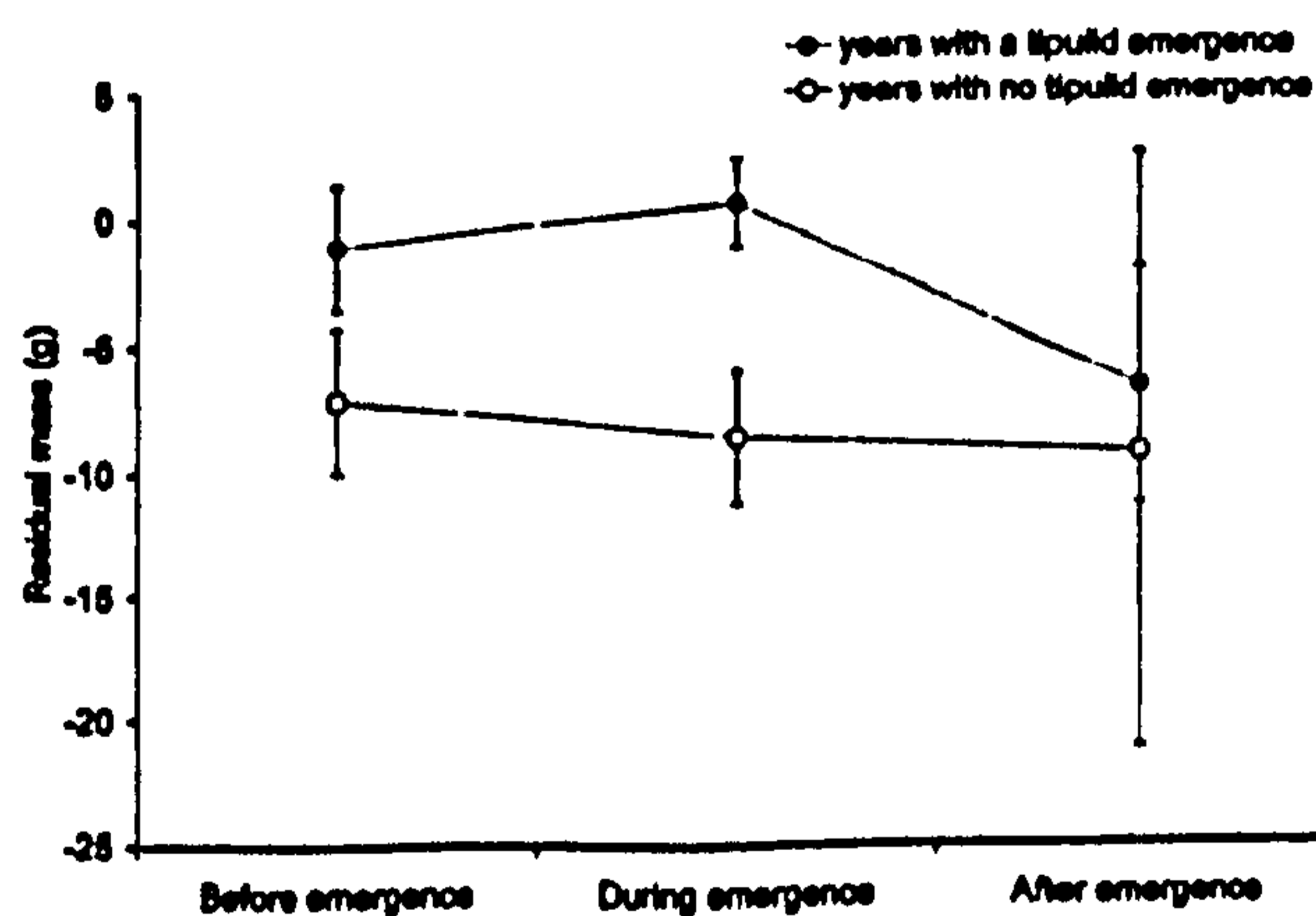


Fig. 3. Variation in the residual mass of nesting male dotterel with *Tipula montana* availability (means  $\pm$  95% c.i., mass corrected for all factors in Table 1 except for *T. montana* availability). In years in which there was a *T. montana* emergence, adult *T. montana* were available during emergences and large, pre-emergence larvae were available before emergences.

tor to balance its energy budget (Moreno 1989a). A lone parent can decrease its reliance on body stores by spending more time foraging, but eggs that are attended less will spend more time below a temperature suitable for development, extending the incubation period and ultimately causing the parent to use more body stores (Løfaldli 1985, Arnold et al. 1995, Tombre and Erikstad 1996, own unpubl. data). Body size is likely to constrain the degree to which incubation can be fuelled from body stores (Harvey et al. 1989, Moreno 1989a, Yerkes 1998). Large waterfowl, for example, may largely or entirely fuel incubation from body stores (e.g. Gabrielsen 1989, Reed et al. 1995) but dotterel commencing incubation have only an estimated mean of 43 g of mass to metabolise before dropping to 68% of their expected mass for body size, when they may become unable to fly. Dotterel, therefore, must fuel the incubation period principally by foraging and supplement the energy budget using body stores when necessary. Even after mass loss through the incubation period, dotterel in our sample were generally able to maintain their body stores well above 68%. However, during prolonged spells of poor weather dotterel may neglect their eggs for periods of many hours or permanently desert them (S. Holt and D. P. Whitfield unpubl.) and this may represent the point at which the parent will not use further body stores to balance an energy-budget deficit. As some birds may have deserted prior to our intended capture, our sample may be biased against individuals that were unable to balance their energy budgets and maintain sufficient body stores to continue to care for the eggs or chicks (Korschgen 1977, Mallory and Weatherhead 1993, Jones 1994).

Uniparental dotterel had smaller body stores than biparental dotterel, as in other shorebird species (Soloviev and Tomkovich 1997, Hegyi and Sasvári 1998). Dotterel incubating alone spent a mean of 18% of their time off the nest (own unpubl. data). At biparental nests, females incubated for approximately 35% of the 94% of the total time that the nest was attended by both parents (D. P. Whitfield and S. Holt unpubl.), giving their mates approximately double the time away from the nest as used by lone males. Other than when disturbed by predators, uniparental males spent virtually all their time off their nest feeding intensely, but off-duty biparental males often spent time loafing (pers. obs.). It is likely, then, that biparental males' masses are not constrained by their energy budgets and that their estimated mean of 6.7% of additional mass approximates an optimum. However, since biparental males' foraging time is less constrained, they may be less likely to experience periods of energetic shortfall so their optimal stores may be smaller than for lone incubators. We have discussed the larger body stores of biparental dotterel in terms of energetic constraint but they could alternatively be a consequence of females choosing to assist males in

better body condition. We cannot evaluate the probability of this alternative explanation: females may only share incubation when they have a low probability of finding a new mate, irrespective of male condition (Emlen and Oring 1977) or may even choose to assist males with smaller body stores if this reduces the high incidence of late-season nest desertions (D. P. Whitfield unpubl.).

In this study, using natural variation in the degree of energetic constraint, we found that mass loss in incubating dotterel was consistent with energetic constraint rather than individual mass optimisation. By experimentally lifting energetic constraints, Cucco and Malacarne (1997) demonstrated mass loss through constraint, whereas most similar studies have found that mass loss is adaptive (Moreno 1989b, Merkle and Barclay 1996, Cavitt and Thompson 1997, Slagsvold and Johansen 1999). What predisposes some species, such as dotterel, to mass loss through energetic constraint while other species are able to follow optimal mass trajectories? As we have already discussed, uniparental care, especially in the absence of mate provisioning, and high energetic costs which, during incubation, will often be determined by the severity of the climate, may compel an individual to supplement its energy budget using body stores. Periods of energetic constraint may occur in species with adaptive patterns of mass loss, but if they occur rarely or if birds can quickly regain lost mass (e.g. Hegyi and Sasvári 1998) because of a mild climate or nest microclimate, high food availability or biparental care, mass loss will not be detected. The optimal mass of an individual balances the costs and benefits of body stores, and adaptive mass loss is most frequently recorded during the chick-rearing phase in species that feed their chicks, when the disadvantages of additional body stores, in terms of the energetic costs of locomotion while collecting food, will be greatest (Freed 1981, Norberg 1981, Croll et al. 1993, Jones 1994, Merkle and Barclay 1996). In dotterel, there is likely to be less variation in the importance of locomotory efficiency with stage of breeding: dotterel frequently fly to make foraging trips from the nest while incubating but, although spending more in terrestrial locomotion when caring for their self-feeding chicks, rarely fly at this stage (pers. obs.). In such species with self-feeding chicks, the adaptive pattern of mass loss after hatch may be less likely to occur or be less marked (Moreno 1989a). In summary, uniparental care without mate provisioning, self-feeding chicks and high energetic costs due to a cold climate may predispose dotterel to a pattern of mass loss through energetic constraint.

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## References

- Andreev, A. V. 1999. Energetics and survival of birds in extreme environments. - *Ostrich* 70: 13-22.
- Arnold, T. W., Anderson, M. G., Emery, R. B., Sorenson, M. D. and de Sobrino, C. N. 1995. The effects of late-incubation body-mass on reproductive success and survival of canvasbacks and redheads. - *Condor* 97: 953-962.
- Bruinzeel, L. W. and Piersma, T. 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in knot *Calidris canutus*. - *Ibis* 140: 323-328.
- Cavitt, J. F. and Thompson, C. F. 1997. Mass loss in breeding house wrens: effects of food supplements. - *Ecology* 78: 2512-2523.
- Cramp, S. and Simmons, K. E. L. (eds). 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. 3: Waders to Gulls. Oxford University Press, Oxford.
- Croll, D. A., Gaston, A. J. and Noble, D. G. 1993. Adaptive loss of mass in thick-billed murrelets. - *Condor* 93: 496-502.
- Cucco, M. and Malacarne, G. 1997. The effect of supplemental food on time budget and body condition in the black redstart *Phoenicurus ochruros*. - *Ardea* 85: 211-221.
- Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. - *Science* 197: 215-223.
- Freed, L. A. 1981. Loss of mass in breeding wrens: stress or adaptation? - *Ecology* 62: 1179-1186.
- Gabrielsen, G. W. 1989. Energy saving in incubating birds. - In: Bech, C. and Reinertsen, R. E. (eds). Physiology of cold adaptation in birds. Plenum Press, New York, pp. 325-328.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D. P. and Thompson, D. B. A. 1993. Diet and habitat use of the dotterel *Charadrius morinellus* in Scotland. - *Ibis* 135: 148-155.
- Gaston, A. J. and Jones, I. L. 1989. The relative importance of stress and programmed anorexia in determining mass loss by incubating ancient murrelets. - *Auk* 106: 653-658.
- Harvey, J. M. 1971. Factors affecting blue goose nesting success. - *Can. J. Zool.* 49: 223-234.
- Harvey, W. F., Hepp, G. R. and Kennamer, R. A. 1989. Body mass dynamics of wood ducks during incubation: individual variation. - *Can. J. Zool.* 67: 570-574.
- Hegyí, Z. and Sasvári, L. 1998. Parental condition and breeding effort in waders. - *J. Anim. Ecol.* 67: 41-53.
- Jones, I. L. 1994. Mass changes of least auklets (*Aethia pusilla*) during the breeding season: evidence for programmed loss of mass. - *J. Anim. Ecol.* 63: 71-78.
- Kálás, J. A. 1986. Incubation schedules in different parental care systems in the dotterel (*Charadrius morinellus*). - *Ardea* 74: 185-190.
- Kálás, J. A. and Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian dotterel (*Charadrius morinellus*). - *Auk* 101: 838-847.
- Kálás, J. A. and Løfaldli, L. 1987. Clutch size in the dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? - *Ornis Scand.* 18: 316-319.
- Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. - *J. Wildl. Manage.* 41: 360-373.
- Løfaldli, L. 1985. Incubation rhythms in the great snipe *Gallinago media*. - *Holarct. Ecol.* 8: 107-112.
- Mallory, M. L. and Weatherhead, P. J. 1993. Incubation rhythms and mass loss of common goldeneyes. - *Condor* 95: 849-859.
- Merkle, M. S. and Barclay, R. M. R. 1996. Body mass variation in breeding mountain bluebirds *Sialia currucoides*: evidence of stress or adaptation to flight? - *J. Anim. Ecol.* 65: 401-413.
- Moreno, J. 1989a. Strategies of mass change in breeding birds. - *Biol. J. Linn. Soc.* 37: 297-310.
- Moreno, J. 1989b. Body-mass variation in breeding northern wheatears: a field experiment with supplementary food. - *Condor* 91: 178-186.
- Norberg, R. Å. 1981. Temporary weight decrease in breeding birds may result in more fledged young. - *Am. Nat.* 118: 838-850.
- Norusis, M. J. 1990. SPSS/PC + Advanced Statistics 4.0. - SPSS Ltd., Gorinchem.
- Piersma, T. and Morrison, R. I. G. 1994. Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high Arctic conditions. - *Auk* 111: 366-376.
- Pulliainen, E. and Saari, L. 1992. Body mass and physical condition of breeding dotterels *Charadrius morinellus* in Finland. - *Oecologia Montana* 1: 1-4.
- Reed, A., Hughes, R. J. and Gauthier, G. 1995. Incubation behaviour and body mass in greater snow geese. - *Condor* 97: 993-1001.
- Ricklefs, R. E. 1974. Energetics of reproduction in birds. - In: Paynter, R. A. J. (ed.). Avian energetics. Nuttall Ornithological Club, pp. 152-297.
- Ricklefs, R. E. and Hussell, D. J. T. 1984. Changes in adult mass associated with the nesting cycle in the European starling. - *Ornis Scand.* 15: 155-161.
- Schamel, D. and Tracy, D. M. 1987. Latitudinal trends in breeding red phalaropes. - *J. Field Ornithol.* 58: 126-134.
- Slagsvold, T. and Johansen, M. A. 1999. Mass loss in female pied flycatchers *Ficedula hypoleuca* during late incubation: supplementation fails to support the reproductive stress hypothesis. - *Ardea* 86: 203-211.
- Soloviev, M. Y. and Tomkovich, P. S. 1997. Body mass changes in waders (*Charadrii*) in a high arctic area at Northern Taimyr, Siberia. - *J. Ornithol.* 139: 271-281.
- Tombre, I. M. and Erikstad, K. E. 1996. An experimental study of incubation effort in high-arctic barnacle geese. - *J. Anim. Ecol.* 65: 325-331.
- Veasey, J. S., Metcalfe, N. B. and Houston, D. C. 1998. A reassessment of the effect of body mass upon flight speed and predation risk in birds. - *Anim. Behav.* 56: 883-889.
- Wendeln, H. and Becker, P. H. 1996. Body-mass change in breeding common terns *Sterna hirundo*. - *Bird Study* 43: 85-95.
- Williams, J. B. 1996. Energetics of avian incubation. - In: Carey, C. (ed.). Avian energetics and nutritional ecology. Chapman & Hall, New York, pp. 375-415.
- Witter, M. S. and Cuthill, I. C. 1993. The ecological costs of avian fat storage. - *Phil. Trans. R. Soc. Lond. B.* 340: 73-92.
- Yerkes, T. 1998. The influence of female age, body mass, and ambient conditions on redhead incubation constancy. - *Condor* 100: 62-68.

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## Chapter 3

# INCUBATION SCHEDULING BY EURASIAN DOTTEREL UNDER ENERGETIC CONSTRAINT

S. Holt, D.P. Whitfield & D.M. Bryant

### Abstract

1. Eurasian dotterel *Charadrius morinellus* breed in cool arctic-alpine environments where the high energetic costs of incubation are usually borne by a single parent. The costs of incubation and the cooling rates of unattended eggs were estimated using an artificial brood patch, nest and eggs. These measurements were used to estimate values for natural nests and to construct models that predicted how dotterel might schedule incubation to enhance their eggs' thermal environment and to vary the costs of incubation. We compared predictions from these models to the incubation scheduling of dotterel recorded in the field.
2. Uniparental nest attendance was constrained by the balance between energetic costs and food intake as attendance decreased with increasing current and past energetic costs and increased when an important prey, *Tipula montana*, was available. Where two parents shared incubation, nest attendance appeared to be independent of costs.
3. Uniparental nest attendance may also have been constrained by dotterel's levels of stored body reserves. Nest attendance declined through the incubation period as birds' reserves were depleted and birds with greater masses (after controlling for structural size and stage of breeding) attended their nests more.
4. The proportion of time that uniparental dotterel could keep their eggs at a temperature suitable for embryonic development was energetically constrained: the eggs of biparental nests spent less time at low temperatures than those of uniparental nests and the amount of time uniparental nests' eggs spent at low temperatures decreased when energetic costs were lower or when *T. montana* were available.

5. Dotterel's improvement in their embryos thermal environment when less energetically constrained was not always achieved by increasing their energetic investment in incubation: neither uniparental dotterel with *T. montana* available nor biparental dotterel increased their energetic expenditure on incubation. However, uniparental dotterel increased their expenditure on incubation when thermostatic energetic costs were lower by making shorter, more frequent trips from the nest.
6. Incubation scheduling appeared to be constrained by the risk of clutch predation: a greater proportion of trips to and from the nest were made after dark on a site where daylight-hunting avian predators were abundant and nocturnal predators scarce. However, the risk of damaging embryos through chilling during feeding trips did not appear to constrain scheduling as the proportion of time that eggs spent at low temperatures increased through the incubation period as the thermal sensitivity of embryos would be expected to increase.
7. Uniparental dotterel, but not biparental dotterel, scheduled their feeding trips to coincide with conditions when their eggs would have cooled more slowly if unattended, thereby improving their eggs' thermal environment and reducing the energetic cost of egg rewarming.
8. Overall the incubation behaviour of dotterel in a cool alpine environment was consistent with their experiencing tight energetic constraints.

## Introduction

High energetic demands for reproduction may constrain the number or quality of young produced per breeding attempt, the frequency of breeding attempts or the parents' longevity, ultimately constraining lifetime reproductive success (LRS, Williams 1996; Monaghan & Nager 1997; Thomson et al. 1998b). Incubation can be an energetically costly stage of breeding (Thomson et al. 1998a; Bryan & Bryant 1999; Reid et al. 1999), especially if the clutch mass is large relative to the parent's body size (Biebach 1984; Haftorn & Reinertsen 1985; Løfaldli 1985; Coleman & Whittall 1988; Siikamaki 1995) and where much heat is lost from the clutch because of a cool nest microclimate (Walsberg 1983; Biebach 1984; Haftorn & Reinertsen 1985; Haftorn & Reinertsen 1990; Thomson et al. 1998b; Reid et al. 2000) or the pattern of incubation scheduling (Vleck 1981a; Vleck 1981b; Webb & King 1983).

If incubation is potentially costly then behavioural mechanisms that reduce costs could increase LRS (Bryan & Bryant 1999). To maximise its LRS, a parent must balance the conflicting demands of maintaining a suitable thermal environment for the development of its embryos while managing its energy budget to ensure its own survival (Carey 1980; Davis et al. 1984; Cartar & Montgomerie 1985; Drent et al. 1985; Løfaldli 1985; Erikstad et al. 1998; Hainsworth et al. 1998). In a cold climate, resolution of this conflict can be especially difficult as the parent's energetic costs of both thermoregulation and steady-state incubation are likely to be high (Piersma & Morrison 1994; Andreev 1999). Additionally, the cooling rate of unattended eggs will be greater in colder climates, increasing the energetic cost of egg rewarming that the parent has to bear on its return to the nest and potentially exposing the eggs to low temperatures below which development may pause, or which may even be damaging to the embryos (Webb 1987). This allocation conflict will be most severe in uniparental incubators, where the thermal requirements of the embryos will restrict the foraging time available to the parent to meet its energetic costs (White & Kinney 1974; Carey 1980; Morton & Pereyra 1985; Løfaldli 1985; Williams 1996; Hainsworth et al. 1998; Bryan & Bryant 1999; Reid et al. 1999).

The conflict between foraging and incubation may result in egg neglect, chilling damage to the embryos, extension of the incubation period, nest desertion, a reduction in attendance or an increase in parental mass loss or risk of mortality, (Harris 1970; Korschgen 1977; Ankney & MacInnes 1978; Konratiev 1982; Sibly & McCleery 1985; Jones 1987; Haftorn 1988; Paladino 1989; Moreno 1989b; Hepp et al. 1990; Mallory & Weatherhead 1993; Reed et al. 1995; Sanz 1995; Erikstad et al. 1998; Fernández & Reboresda 2000; Holt et al. 2002). If a parent spends more time foraging to make up an energetic shortfall this may increase the amount of time that the embryos spend below a temperature suitable for development, extending the incubation period and ultimately causing greater depletion in the parent's body reserves as well as reducing hatching success (Vleck & Kenagy 1980; Tombre & Erikstad 1996). However, there may be periods of poor conditions, such as severe weather, when a parent may be compelled to reduce nest attendance, even at the cost of increased egg exposure (Løfaldli 1985). Conversely, if energetic constraint is lessened by an increase in foraging efficiency through, for example, improved food availability, parents may be able to increase the time they spend on the nest. Breeding birds may supplement their energy budgets using stored body reserves (Reed et al. 1995; references in Eichholz & Sedinger 1999; Holt et al. 2002), so that birds with more reserves may be less constrained in their expenditure on incubation (Erikstad 1986; Martin 1987; Harvey et al. 1989; Hegyi & Sasvári 1998; Eichholz & Sedinger 1999).

One important way that the conflict between incubation and foraging may be lessened is by incubation scheduling: for any given level of nest attendance the overall energetic cost of incubation will vary dependent on the pattern of incubation scheduling (Vleck 1981a; Vleck 1981b; Webb & King 1983). A parent can schedule its feeding trips to coincide with favourable weather when the cooling rate of the exposed eggs will be lower (Webb & King 1983; Løfaldli 1985), decreasing the cost of rewarming (Cartar & Montgomerie 1987) and reducing the amount of time that the eggs spend below a temperature suitable for development (the physiological zero temperature or PZT, Drent 1975). A parent may also change the cost of incubation, irrespective of weather conditions, by varying the frequency and duration of individual feeding trips for a given level of nest attendance. Exposed eggs

follow a negative exponential cooling curve (Ricklefs 1974) so that heat is lost fastest at first: a parent may reduce its egg rewarming costs by making fewer but longer feeding trips.

There may be constraints that mean that incubation scheduling cannot be optimised solely in terms of the parent's energetic expenditure. Firstly, fewer, longer trips may result in the eggs spending longer below the PZT than the same total duration of shorter trips, potentially increasing the incubation period. Trip length must, then, trade-off egg rewarming costs against the time eggs spend below a temperature suitable for egg development, and the balance of this trade-off is likely to vary with the degree of energetic constraint experienced by the parent (Vleck 1981a; Haftorn 1988).

Secondly, in many bird species, relatively short periods of chilling may kill or have sub-lethal detrimental effects on the embryos (Webb 1987) so that the pattern of incubation may be constrained to prevent severe chilling. The sensitivity of embryos to chilling can change through the incubation period, generally increasing towards hatch (MacMullan & Eberhardt 1953; Batt & Cornwell 1972; Deeming & Ferguson 1991), potentially varying the limits on trip length, so that incubation scheduling might vary through the incubation period.

The third main potential constraint on incubation scheduling is avoidance of egg-predation, which is often a main cause of avian breeding failure (Ricklefs 1969). The scheduling of trips may vary with daily patterns of predator activity if the parent's activity (around the nest during feeding trips) increases the probability of a predator finding the nest (Erikstad et al. 1982; Wiebe & Martin 1997; Martin & Ghalambor 1999), or if the presence of the parent at the nest can deter predators (Drent 1970; e.g. Harvey 1971; Inglis 1977). If the risk of egg-predation is increased by parental activity and the parent can feed efficiently at night we would predict that a greater proportion of trips to and from the nest would be made during darkness if daytime-hunting predators are abundant than if they are scarce.

The Eurasian dotterel *Charadrius morinellus* nests on the ground in the cool arctic-alpine zone, where the energetic costs of thermoregulation and incubation are likely to be high



(Piersma & Morrison 1994; Andreev 1999). As most nests are cared for by the male alone (Cramp & Simmons 1983), the parent also has limited foraging time in which to recoup these high costs (Kálás 1986) so we would predict that the conflict between care of the eggs and self is particularly pronounced in uniparental dotterel. A proportion of dotterel nests have biparental incubation, which gives the carers both smaller energetic costs of incubation and greater foraging time to recoup costs, so that biparental dotterel will be less energetically constrained than uniparental dotterel. This variation in the parental care of dotterel, and the consequent variation in the degree of energetic constraint experienced, provides a useful tool for investigating adaptations to the degree of energetic constraint experienced during incubation. This study determines whether there is a conflict between care of eggs and self in dotterel and investigates how dotterel may resolve this conflict via variation in their incubation scheduling. The following predictions are tested:

1. Uniparental nest attendance is energetically constrained so that daily nest attendance will be higher when energetic costs are low or food availability is high, but the attendance at biparental nests will be independent of such variation in conditions.
2. At biparental nests and at uniparental nests in favourable conditions, when energetic costs are low or food availability high, dotterel will expend more energy on incubation and schedule incubation so that the eggs rarely cool below the PZT.
3. Incubation scheduling will be constrained by the risk of clutch predation so that, since dotterel can feed at night (Cramp & Simmons 1983), a greater proportion of trips will be at night if visually hunting avian egg-predators are more important than nocturnal predators.
4. Thermal sensitivity of avian embryos may vary with the stage of incubation, changing the limits on trip length. However, dotterel embryos are extremely tolerant of chilling throughout the incubation period (Chapter 4), so we predict that stage of incubation should have no influence on the degree of chilling that the eggs are exposed to: the percentage of time the eggs spend below the PZT will be independent of the stage of incubation.

5. To minimize the energetic cost of egg rewarming and the time eggs spend below the PZT, dotterel will schedule incubation so that trips are made in conditions when eggs would cool more slowly if unattended.

To test predictions of how incubation scheduling varies with the energetic costs, we needed estimates of the cost of incubation. Current biophysical models appear to only poorly describe the energetic costs of incubation (Croxall 1982; Vleck 1981a; Walsberg 1983) so we derived an empirical model of how costs vary with weather conditions based on measurements from an artificial brood patch and nest.

## **Methods**

Data on incubation scheduling were collected in 1997 and 1998 from two low-alpine (Horsfield & Thompson 1996) sites (denoted B and D, Holt et al. 2002), separated by 8km, in the Central Highlands of Scotland. Dotterel are vulnerable to illegal egg collectors so site locations are not given. The observer was licensed to study nesting dotterel. The date that a clutch was initiated (first egg date) was observed, estimated from hatch date (assuming a 28 day period from first egg laid to last chick hatched, Cramp & Simmons 1983; D.P. Whitfield unpublished data) or estimated from an equation relating egg density to days until hatch (derived from measurements of clutches of known hatch date; D.P. Whitfield unpublished data).

## **NEST ATTENDANCE**

Nest attendance (the proportion of time nests were incubated, Norton 1972) was recorded for 46 nests using a small flexible temperature probe fixed at the centre of the nest, logged at 35s intervals by a Tinytag datalogger (Gemini Data Loggers (UK) Ltd, Chichester, UK). The accuracy of the nest attendance data obtained from nest temperature probes was checked by opportunistically making visual records of attendance at logged nests. Birds were recorded as sitting (seen on the nest), absent (no dotterel sitting or a uniparental dotterel seen off the nest), going onto the nest or coming off the nest. In 98.9% of 91 cases from 29 nests a

dotterel was correctly identified as sitting. In the single incorrect case the bird was sitting but the nest was partially flooded. The nest was correctly classed as unattended in 100% of 58 cases from 26 nests. In 65% of 35 cases from 21 nests the time the bird left the nest was identified to the correct 35s logging interval. In a further 26% of cases the time the bird left the nest was one 35s interval out, in 6% two 35s intervals out and in 3% four 35s intervals out. In 55% of 32 cases from 17 nests the time the bird went onto the nest was identified to the correct 35s logging interval. In a further 39% of cases the time the bird returned to the nest was one 35s interval out and 6% two 35s intervals out. A further four nest absences when the bird was seen leaving the nest and one where the bird was seen going on were missing in the logged nest attendance data. When the nest attendance data were re-examined all these absences were probably less than 3.5 minutes long. These observations illustrate that nest attendance data were accurate since, in addition, i) data were collected during the day when the difference between nest and ambient temperature was least marked and so the nest temperature changes used to identify absences from the nest were slower (Hainsworth et al. 1998) and ii) some correct nest-absence durations were probably recorded as incorrect when the data logger and the observer's watch were poorly synchronised. The measure of overall nest attendance included only absences from the nest of at least 140 seconds. Dotterel rarely feed during such short nest absences (Kálás 1986) and it is likely that shorter trips would not be accurately detected from temperature traces at all nests under all weather conditions (Hainsworth et al. 1998). Embryo temperature would be unlikely to fall below the PZT during this time: PZT lies between 20 and 27°C in chickens (Wilson 1991), though it is likely to vary between species (Webb 1987).

## WEATHER RECORDING

Wind speed was recorded at 1.45m above ground level at 1.35 min intervals by a Kestrel anemometer (Davis Instruments, Hayward, USA) attached to a LogIt datalogger (DCP Microdevelopments Ltd., Cambridge, UK) on site B. A running mean of three consecutive instantaneous wind speed records was used in analyses. Wind speed was also scored three times a day in the field (morning, afternoon and evening) on the Beaufort scale and

measurements were occasionally made 1.45m above ground level using a Kestrel handheld anemometer (Nielson-Kellerman, Chester, USA).

Shaded air temperature at 1.2m above ground and ground temperature at 0.1m below the surface were recorded at between 1.0 and 3.2 min intervals by thermistors attached to Tinytag or LogIt dataloggers on sites B and D.

Light intensity was recorded by LogIt light sensors and dataloggers on sites B and D, at 1.35 to 3.2 min intervals. These were calibrated against a CM6 pyranometer (Kipp & Zonen, Langworth, UK) to a scale in  $Wm^{-2}$  (the light sensors were not sensitive to infrared radiation).

Precipitation (rain or mist) was recorded on sites B and D at 40s intervals using a Model 237 leaf wetness sensor (Campbell Scientific Inc., Logan, USA), mounted at an angle of 60° at 1.32m above ground level and attached to Tinytag dataloggers. The leaf wetness sensors were correct in 94% of 98 spot field calibrations when it was dry and 93% of 27 when raining and/or misty.

There were occasional gaps in the logged weather records due to logger failure. Where data were available from the other site these were used (means of 13.0% of records of solar radiation, 4.3% of air temperature and 1.9% of precipitation for sites B and D, 0.0% of ground temperature for site D, all ground temperature data for site B, all wind speed data for site D). These missing data were estimated from calibrations calculated from when data were logged on both sites (sites were either both dry or both rainy and/or misty in 82% simultaneous records, and one site predicted 96.6%, 80.9% and 58.3% of the variation in the shaded air temperature, solar radiation and wind speed, respectively, on the other site). For the mean of 7.4% of the time when no wind speed data were recorded on either site, data from the Heriot-Watt University's Cairngorm weather station were used, corrected using a calibration that explained 41.3% of variance in wind speed. Alternatively, wind speed was extrapolated from field estimates (explaining 35.7% of variation, 12.0% of records) or from hand-held anemometer measurements (mean of 0.4% of records). Gaps in the solar radiation record

(mean of 3.6% of records) and temperature records (mean of 0.4% of records) were filled by mean diurnal patterns of days within five days of the missing period that had similar amounts of cloud cover. When ground temperature was not recorded (a mean of 5.8% of records), it was estimated from air temperature, using a calibration that explained 68.1% of variation.

## ENERGETIC COSTS OF INCUBATION

To estimate energetic costs, incubation was partitioned into the three stages of steady-state incubation, the cooling of the eggs while unattended during trips and the rewarming of the cooled eggs on the birds return to the nest. For hypothesis testing, daily energy expenditure on incubation was estimated by combining the costs of steady state incubation and egg re-warming, calculated for the pattern of incubation scheduling recorded for a nest in the current weather conditions. The mean daily cost of constant steady-state incubation (used as an index of the potential energetic cost of incubation) is calculated from current ground temperature.

## STEADY-STATE INCUBATION

The energetic costs of steady-state incubation were estimated by measuring the amount of energy used by an artificial brood patch to maintain the core egg temperature of an artificial clutch at 35.5°C. The artificial brood patch consisted of 75mm diameter electric heat pad run at 3.1W, with a layer of heat transfer compound below, enclosed at the bottom by polythene film. A thermister recorded the temperature inside the heat transfer compound. The artificial brood patch was insulated around the sides and top with foam and expanded polystyrene. To mould the brood patch to fit the eggs it was stored with a plaster cast of the top 7mm of a clutch of eggs pressed into it. During use, a 907g weight was placed on top of the artificial brood patch to ensure good contact with the eggs. Foam film covered the lower brood patch surface except for the areas of egg contact. Charadriiformes are estimated to be able to cover around one fifth of their eggs' surface area with their brood patches (Baerends et al. 1970).

The surface area of dotterel eggs was estimated by measuring the proportions of six published photographs of eggs (Hollom 1980; Cramp & Simmons 1983). The cap end was

approximately hemispherical (the distance from the broadest point to the cap end was  $1.19 \pm 0.12$  times the radius at the broadest point). The remainder of the egg was modelled as a series of seven cone sections (Paganelli et al. 1974). From this model of egg shape, the surface area of an average sized dotterel egg was estimated to be  $3165\text{mm}^2$ . As the cap end of the egg usually lies highest in the nest (pers. obs.) the section of the egg in contact with the brood patch was assumed to be part of a sphere so, for 20% of each egg to contact the brood patch, the brood patch should touch the top 7.3mm of each egg.

The artificial clutch of eggs consisted of three dotterel eggshells (deserted eggs collected under license) filled with a mean air-dry mass of 17.8g of plaster of paris (the mass of a freshly laid average sized egg was estimated to be 17.4g from the relationship between egg density and days until hatch). A thermister was fixed in the core of one egg (the 'control' egg). The clutch was placed in an artificial nest 95mm diameter and 45mm deep (in 405 nests on 9 sites in Scotland mean nest diameter was 96mm and mean depth 46mm), lined with 7.5g of the lichen *Cladonia uncialis* (mean air-dry nest lining mass was 8.4g for 317 nests on 9 sites and *Cladonia uncialis* is a preferred nest lining material, Nethersole-Thompson 1973; S. Holt et al. unpublished data) in a semi-cylindrical sod of *Racomitrium lanuginosum* heath (a preferred nesting habitat, Galbraith et al. 1993) approximately 220mm long by 220mm diameter. A temperature probe was embedded in the sod, c. 20mm from its bottom to measure 'ground' temperature and a shaded thermister was placed c.150mm above the sod to measure air temperature.

Incubating Charadriiformes appear to fill the gaps between and around their eggs with their belly feathers (Baerends et al. 1970; Drent 1970) and this may insulate the eggs and so reduce the cost of steady-state incubation. To simulate this a piece of foam pierced with a hole for each of the eggs and that left the top 7mm of the eggs exposed to the brood patch was placed in the nest. Using foam to fill the gaps between and around eggs gave similar costs of steady-state incubation as when the gaps between the eggs were filled with 0.7g of belly feathers collected from fresh raptor kills of adult dotterel (at air temperatures of between 6 and 7°C steady-state incubation required  $0.93 \pm 0.19\text{W}$  with feathers, measured three times,

0.90±0.04W with foam, measured 18 times). The foam also ensured that the eggs were held in a constant arrangement that matched the form of the brood patch.

A SwitchIt controller (DCP Microdevelopments Ltd., Cambridge, UK) switched the heat pad on and off to maintain the core egg temperature around 35.5°C and, to calculate the power used, the current to the heat pad was recorded by a LogIt datalogger. To estimate and so subtract the amount of heat lost through the top and sides of the artificial brood patch its lower side was insulated by sealing it to a 20cm thick block of expanded polystyrene and measured the amount of power used to maintain it at its mean operating temperature of 41.1°C through the range of air temperatures used.

The costs of steady-state incubation were measured in a temperature-controlled chamber to give 'ground' temperatures of between 1.2°C and 31.8°C, covering most of the range of temperature dotterel experienced during incubation. The costs of steady-state incubation were also measured for clutches of one and two eggs. During measurements for smaller clutch sizes, the spare brood patch depressions were covered by foam film and the eggs were enclosed in foam that had the appropriate number of holes for the clutch size.

The power required for steady-state incubation increased significantly with decreasing ground temperature and with clutch size (GLM: ground temperature  $F_{1,34}=359.900$ , partial  $R^2=0.914$ ,  $P<0.001$ ; clutch size  $F_{1,34}=4.579$ , partial  $R^2=0.119$ ,  $P=0.040$ , Fig. 1). The GLM gave the following relationship (equation 1):

$$\text{power (Watts)} = -0.20174 + 0.032522 \cdot (35.5 - \text{ground temperature}) + 0.05886 \cdot \text{clutch size}$$

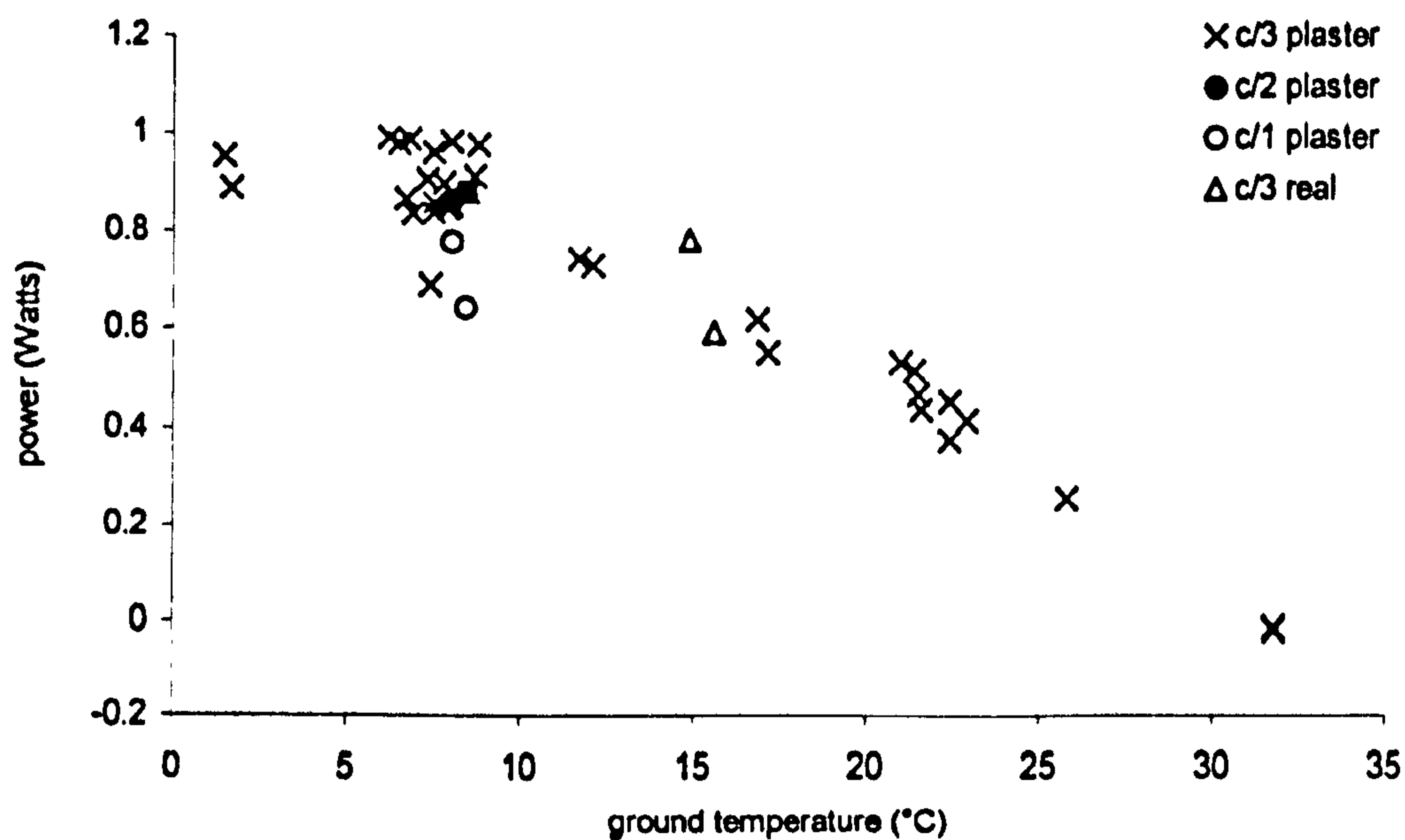


Figure 1. Variation in the power required for steady state incubation with ground temperature and clutch size for plaster-filled and real eggs.

The same apparatus was used to measure the cost of steady-state incubation for a clutch of three real, freshly deserted dotterel eggs, into one of which was inserted a thermister, the hole resealed with beeswax. The cost of steady-state incubation was similar for plaster-filled and real dotterel eggs (Fig. 1). There was no significant embryonic development prior to desertion in these real dead eggs and they probably most closely represented the thermal impedance and resistance of live eggs early in incubation before embryonic circulation decreases impedance and resistance, and changes in the egg contents increase impedance (Turner 1994a). In live eggs, embryonic metabolism might decrease a parent's energetic cost of incubation (Drent 1970) but this is probably cancelled out by the increased rate of heat loss due to embryonic circulation (Turner 1991).

The power required for steady-state incubation at different ground temperatures was estimated from the equation 1. We made several assumptions to arrive at this estimate:

1. We used the value from Baerends et al. (1970) for the proportion of the eggs in contact with the brood patch but this may vary between species, affecting the rate of heat loss from the eggs and so the cost of steady-state incubation, although the effect may be small (Turner 1991). The proportion of the egg covered is unlikely to vary with



clutch size as dotterel have three discrete brood patches so a bird is unlikely to be able to move spare brood patch area into contact with eggs in a one or two egg clutch.

2. We used a target core egg temperature of 35.5°C in our measurements. A dotterel's costs of steady-state incubation may be higher or lower than estimated if their core egg temperature is substantially different from the 35.5°C used. There may be some variation in core egg temperature within shorebirds, although some of this is probably due to differences in measuring methods (Drent 1975; Haftorn 1988). However, the range of temperatures over which embryos of most species can develop is narrow (between 35.0°C and 40.5°C, reviewed in Haftorn 1988) so that 35.5°C is probably a reasonable estimate. There is some evidence that some species may not always strive for the optimal temperature for development and instead sometimes adjust the 'tightness of sit' to reduce heat transfer to the eggs and hence egg temperature (White & Kinney 1974; Morton & Pereyra 1985) or reduce egg temperature through torpor (Vleck 1981b). In clutches with a large cross sectional area relative to that of the sitting parent, individual eggs may at times experience lower temperatures through poor contact with the brood patch. We cannot tell whether dotterel adjust their 'tightness of sit' but it seems unlikely that parts of the clutch need to be in poor contact with the brood patch as, although dotterel's fresh clutches are about 43% of their body mass, the small clutch size probably gives a smaller cross sectional area than a larger clutch of the same total mass would have.
3. The foam insulation around the eggs simulated fluffed belly feathers. While dotterel might not fill the gaps between eggs with feathers, the effect of the inclusion of foam on the costs of steady-state incubation was not great (at air temperatures of between 6°C and 7°C steady-state incubation required  $1.07 \pm 0.05W$  with no foam, measured twice,  $0.90 \pm 0.04W$  with foam, measured 18 times).
4. In all measurements the eggs were arranged with their cap ends pointing out. This arrangement was the most frequent egg arrangement recorded in the field, accounting for 18% of 11 nests. However, dotterel's eggs are arranged in the nest in various permutations of cap end pointing outwards, side pointing outwards and,

rarely, cap pointing in (pers. obs.). Different arrangements may result in different amounts of contact between eggs and so different effective surface areas over which heat can be lost. However, as the eggs are relatively loosely packed in all arrangements, egg arrangement is unlikely to have a great effect on the rate of heat loss.

#### EGG TEMPERATURE WHILE UNATTENDED

After at least an hour of steady-state incubation the artificial brood patch was removed and the plaster-filled eggs subjected to simulated weather conditions, while simultaneously recording the core temperature of the control egg. Air temperature (in a temperature controlled chamber, values between 1.3°C and 32.1°C), wind speed (in a wind tunnel, values between 0 ms<sup>-1</sup> and 3 ms<sup>-1</sup> at 0.02m above ground level) and precipitation were varied (dry or immediately sprayed once using a mister that delivered 0.00147 ± 0.00019 gmm<sup>-2</sup> of water at air temperature, equivalent to a 9 minute long moderate shower, (HMSO 1982). The effect of solar radiation on egg cooling rate was estimated by simultaneously recording the temperatures of an egg exposed to solar radiation and one protected from solar radiation by a louvered radiation shield, outdoors within a wind shield. Air temperature was recorded and the heating effect of solar radiation (°Cs<sup>-1</sup>) was taken to equal the cooling rate for that air and the shaded equilibrium egg temperature difference estimated from laboratory measurements in the absence of solar radiation. The effect of different weather variables on the cooling rate of a body may be synergistic (Calder & King 1974) so egg cooling rates were measured for a range of permutations of weather variables. Again, eggs were arranged with their caps pointing outwards. Cooling rate was measured 54 times for a clutch of three eggs, five times for two eggs and four times for one egg.

Exposed eggs' temperatures followed Newton's cooling curve (equation 2):

$$T_t = e^{-ct}(T_i - T_{eq}) + T_{eq}$$

where  $T_t$  is temperature at time  $t$ ,  $c$  is the egg cooling coefficient,  $T_i$  is the initial egg temperature of 35.5°C and  $T_{eq}$  is the equilibrium egg temperature. The cooling coefficient (s<sup>-1</sup>) for each of the cooling curves was calculated by fitting a least squares linear regression to

equation 2 rearranged as  $\ln((T_t - T_{eq}) / (T_0 - T_{eq})) = -t \cdot c$ . The analysis was confined to the first ten minutes of cooling, as wet eggs did not dry in that time and small fluctuations in the temperature of the chamber will have least affected the rate of cooling in this period when cooling was fastest. This method of estimating cooling coefficients is sensitive to equilibrium egg temperature but equilibrium egg temperature was not always recorded and, when recorded, varied with fluctuations in the chamber temperature. Equilibrium egg temperature was instead estimated by repeating the linear regression with different values of  $T_{eq}$  until a value was obtained whose model explained most variation. The relationship between equilibrium egg temperature and measured air temperature was estimated using linear regression ( $F_{1,53} = 1123.30$ ,  $P < 0.001$ ,  $R^2 = 0.955$ , equilibrium temperature =  $2.605 + (0.927 \cdot \text{air temperature})$ ).

The cooling rates of two real, deserted clutches were measured using the same apparatus under dark, dry, still conditions. The cooling coefficient of a clutch of three real eggs was  $0.0005831 \pm 0.0000681 \text{ s}^{-1}$ , 33.3% ( $\pm 27.8\%$  to  $39.4\%$ ) of that of plaster-filled eggs under the same conditions so to derive the cooling coefficients of real eggs under different weather conditions we multiplied the coefficient for plaster-filled eggs by 0.333. Plaster and eggs have similar thermal conductances (Ward 1990) and, consistent with this, the power for steady-state incubation was similar for real and plaster-filled dotterel eggs (Fig. 1). The difference between the cooling coefficients of real and plaster-filled eggs is probably attributable to their different specific heat capacities (SHC) as the SHC of plaster filled eggs was 45% ( $\pm 35\%$  to  $58\%$ ) that of real eggs.

We then used GLM to determine the effects of weather variables on the cooling coefficients estimated for real eggs. The number of measurements of cooling coefficients gave insufficient statistical power to include many interaction terms so, since precipitation is likely to interact with wind speed and temperature, we derived separate models for wet and dry conditions. When dry, the cooling coefficient increased approximately linearly with wind speed until levelling off at between  $1.5$  and  $2 \text{ ms}^{-1}$  (Fig. 2). To linearise the relationship, for inclusion in the overall model describing the relationship between cooling rate and weather variables, we

substituted  $1.72\text{ms}^{-1}$  for wind speeds exceeding it. When the eggs were wet, cooling coefficients remained approximately constant up to a wind speed of  $1\text{ms}^{-1}$  and then increased (Fig. 2). To linearise the relationship and retain its direction we substituted  $-1\text{ms}^{-1}$  for wind speeds less than  $1\text{ms}^{-1}$  and used the function  $-1/\text{wind speed}$  for greater speeds. When wet, the cooling coefficient appeared to still be increasing with wind speed at our highest experimental speed of  $3\text{ms}^{-1}$  and we continued to use the  $-1/\text{wind speed}$  function when estimating cooling coefficients for higher wind speeds. This may lead to inaccuracy in the estimates of cooling coefficients for the 15.3% of dotterel incubation time with wet, very windy conditions.

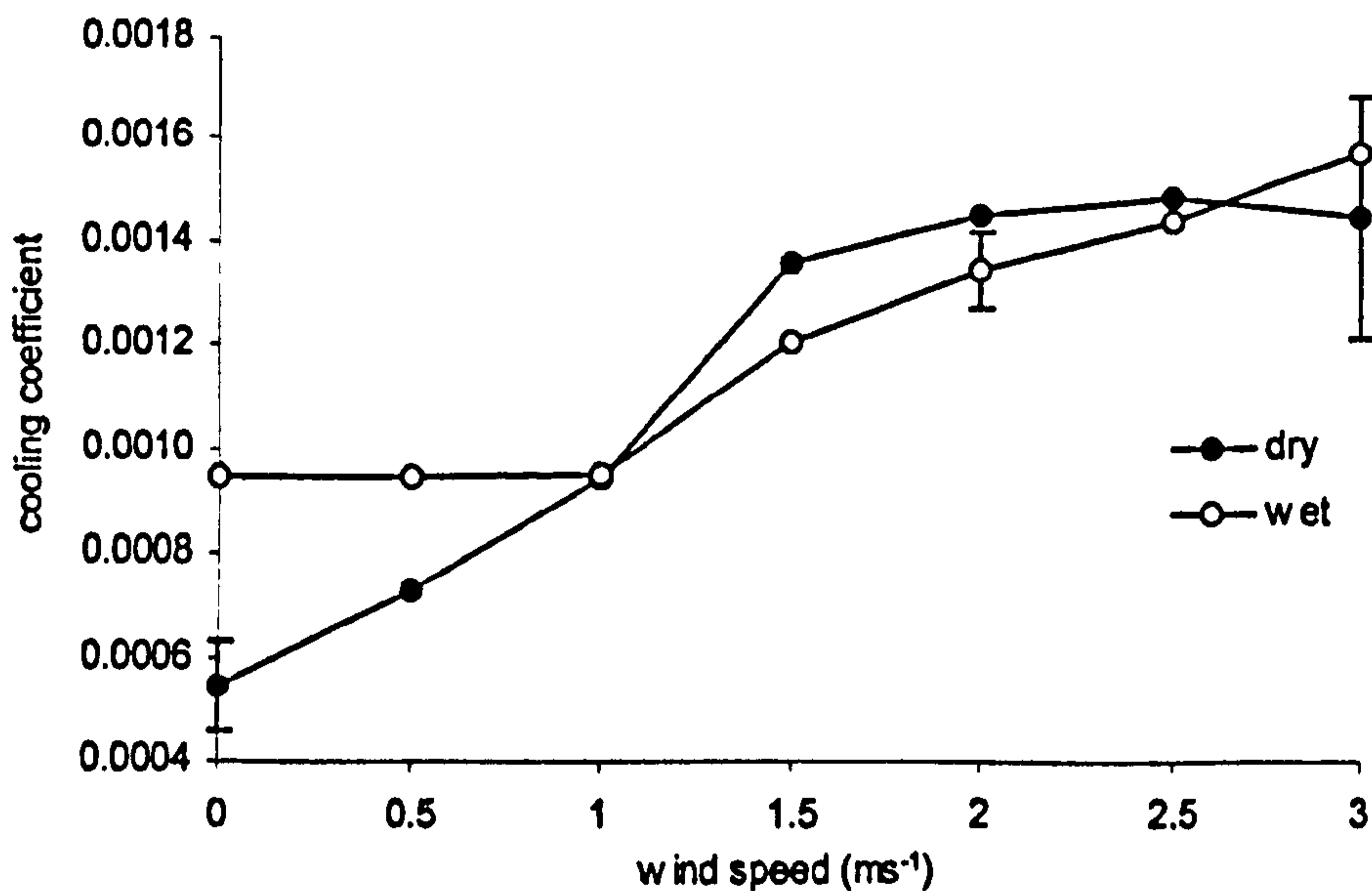


Figure 2. Variation in the estimated egg cooling coefficients for wet and dry clutches of three real eggs with wind speed (mean  $\pm$  95% c.i., at air temperatures between  $5^{\circ}\text{C}$  and  $8^{\circ}\text{C}$ ).

When dry, the cooling coefficient was independent of air temperature but increased with wind speed and there was a significant, positive interaction between wind speed and air temperature (GLM: air temperature  $F_{1,22}=0.37$ ,  $P=0.552$ , function of wind speed  $F_{1,22}=54.17$ ,  $P<0.001$ , air temperature\*function of wind speed  $F_{1,22}=7.09$ ,  $P=0.015$ , overall  $R^2_{adj}=0.928$ , cooling coefficient =  $5.336 \cdot 10^{-4} + (2.557 \cdot 10^{-6} \cdot \text{air temperature}) + (4.234 \cdot 10^{-4} \cdot \text{function of wind speed}) + (8.839 \cdot 10^{-6} \cdot \text{function of wind speed} \cdot \text{air temperature})$ ). When wet, the cooling coefficient increased significantly with air temperature and wind speed and there was a

significant positive interaction between wind speed and air temperature (GLM: air temperature  $F_{1,18}=31.76$ ,  $P<0.001$ , function of wind speed  $F_{1,18}=22.91$ ,  $P<0.001$ , air temperature\*function of wind speed  $F_{1,18}=9.84$ ,  $P=0.007$ , overall  $R^2_{adj}=0.925$ , cooling coefficient= $1.549 \cdot 10^{-3} + (4.109 \cdot 10^{-5} \cdot \text{air temperature}) + (7.041 \cdot 10^{-4} \cdot \text{function of wind speed}) + (3.103 \cdot 10^{-5} \cdot \text{function of wind speed} \cdot \text{air temperature})$ ). Overall, the models explained 94% of the variance in cooling coefficients.

### COST OF RE-HEATING EGGS

The thermal capacity of eggs heated by a brood patch in a cool environment where a temperature gradient develops through the egg can be significantly less than their thermal capacity when the whole egg is at the same temperature as the core (gravimetric thermal capacity, Turner 1997): egg rewarming may require less energy than might be calculated from gravimetric thermal capacity. To enable us to estimate the cost of reheating cooling eggs we measured the thermal capacity of eggs under conditions should have recreated the temperature gradients they would develop during natural incubation. We measured the thermal capacity of two real, deserted eggs, each with a temperature probe inserted, after a bout of steady-state incubation within a clutch of three real eggs by the artificial brood patch, by immediately placing the eggs in a known mass of water in an insulated flask and measuring the change in temperature of the water and eggs. The thermal capacity of an 18.1g egg was  $2.801 \pm 0.419 \text{ jg}^{-1} \text{ } ^\circ\text{C}^{-1}$  at ground temperatures between 6.2 and 8.0°C and  $2.622 \pm 0.080 \text{ jg}^{-1} \text{ } ^\circ\text{C}^{-1}$  between 16.0 and 16.4°C (measured three times for each temperature range). The measured thermal capacity where there was no thermal gradient (after incubation in a water bath at 35.5°C) was  $3.215 \pm 0.378 \text{ jg}^{-1} \text{ } ^\circ\text{C}^{-1}$  (measured three times). As we did not have sufficient data to detect any variation in thermal capacity with ground temperature we used the mean value of  $2.712 \text{ jg}^{-1} \text{ } ^\circ\text{C}^{-1}$  measured between 6.2 and 16.4°C to calculate the cost of clutch re-heating at all ground temperatures.

We estimated the cost of re-heating a cooled clutch as clutch size \* mean egg mass \* thermal capacity \* (35.5-estimated core egg temperature before heating). This calculation assumes that temperature at the core of an egg after a period of cooling is a good measure of its mean

temperature. The thermal capacity of dotterel eggs incubated by an artificial brood patch in an artificial nest at air temperatures between 6.2°C and 16.4°C was a mean of a mean of 84% ( $\pm$  95% c.i. 70% to 103%) of their gravimetric thermal capacity. This may be a greater percentage than in domestic fowl *Gallus gallus*, whose 55g eggs incubated by an artificial brood patch had a thermal capacity one third of their gravimetric thermal capacity (Turner 1997), because smaller eggs have smaller temperature gradients. (Turner 1991).

#### COST OF INCUBATION SHIFTS

To estimate the energetic cost of a complete incubation shift we calculated the amount of time required to re-heat the eggs and then costed the remaining time as steady-state incubation. To allow estimation of the amount of time taken to re-heat eggs, we estimated power input to eggs during the initial phase of reheating of real nests, when temperature increased approximately linearly with time. We used nest probe temperature as an index of egg temperature for reheating records where the probe appeared to be principally influenced by egg temperature rather than brood patch or nest air temperature (as the probe did not exceed 35°C during the preceding or following 24 hours and had a stable temperature while attended). We used only records of egg re-heating after long inattentive periods in dull weather when the eggs and probe would have equilibrated to similar temperatures. We assumed that eggs were re-heated to 35.5°C and that, during re-heating, changes in probe temperature were linearly related to changes in egg temperature.

The mean power for egg re-warming was  $2.53 \pm 0.37W$ , so the estimated time for re-heating a clutch was: thermal capacity \* clutch size \* mean egg mass \* (35.5-cooled core egg temperature) / 2.53. However, as the eggs were heated up their rate of heat loss to the ground would increase, until a stable temperature gradient and steady-state incubation was achieved. As egg temperature appeared to increase approximately linearly for most of the temperature rise during rewarming we assumed a constant rate of heat delivery and power production for rewarming. Supporting this approach, Tøien (1989) suggests that the greater heat required to rewarm colder clutches may be delivered principally by extending the rewarming period rather than increasing the rate of heat transfer and Drent et al. (1985) found that re-warming time

was related to the logarithm of trip length so that it was probably proportional to egg temperature at the end of the trip.

During the re-heating phase we assumed that egg temperature increased linearly and we estimated the rate of heat loss from the model for steady-state incubation (equation 1), substituting the estimated current core egg temperature for 35.5 in the term for the difference between core egg and ground temperature. This estimate assumes that the rate of heat loss increases in direct proportion to increasing core temperature during re-heating. A time lag in heat reaching the most distant parts of the egg (Turner 1994a) may mean that we overestimated heat loss during early egg re-heating. However, as replacing lost heat may be a significant part of the cost during re-heating (e.g. we estimate it to be 20% of the cost during the 13 minute re-heating of a clutch cooled to 20°C at a ground temperature of 8°C), it is likely to be important in a model of the cost of incubation.

There appears to be an upper limit on thermogenesis, that lies between around 5 and 8 times basal metabolic rate (BMR) or resting metabolic rate (RMR, Table 1). Although we could find no published maximal thermogenesis values for shorebirds, *Calidris alpina*, *C. pusilla*, *C. melanotus* and *C. bairdii* were able to increase their resting metabolic rates between roughly three and four fold as temperatures dropped to around -20°C, without reaching a plateau of maximal thermogenesis (Norton 1973). Using Wiersma & Piersma's (1994) model of the costs of thermoregulation of shorebirds the mean index of the power for thermoregulation for incubating dotterel was  $2.9 \pm 0.1W$  (although we cannot evaluate how the required power is affected by sitting in the nest cup). Adding this to our estimate of 2.53W for egg-rewarming means that dotterel may expend 5.4W or around 5.2 x BMR during rewarming (estimated according to Kersten & Piersma 1986), within the bounds of the values of maximal thermogenesis recorded for other bird species (although egg rewarming may anyway partly be fuelled by an initial drop in the parent's body temperature, Haftom & Reinertsen 1982, so that birds may spread the thermogenesis for egg rewarming over time by bringing their body temperature back up slowly).

## EMBRYONIC METABOLISM

We did not include any effect of embryonic metabolism on egg temperature and the energetic costs of incubation. Heat produced by embryonic metabolism could reduce both the costs of steady-state incubation and rewarming and this reduction might increase as embryos develop through the incubation period (Drent 1970) but the increase in the rate of heat loss through embryonic circulation probably more than cancels this out (Turner 1991). In species such as dotterel, that decrease attendance as egg temperatures drop or weather conditions worsen, a possible explanation for the decline in attendance through the incubation period and the consequent increase in time spent below the PZT is that the increased circulation of the developing embryos increases the cost of incubation (Turner 1991), compelling parents to spend more time off the nest foraging. The energetic cost of incubating turkey *Meleagris gallopavo* eggs with a simulated brood patch increased by roughly three quarters through the incubation period (Turner 1991) but this effect will be far less important in dotterel's smaller eggs where there will be a smaller potential temperature gradient for the embryonic circulation to influence (Turner 1997). Blue tits *Parus caeruleus* increased their energy expenditure while incubating through the incubation period (Haftorn & Reinertsen 1985). However, this may have been a consequence of the parent's increased ability to transfer heat to the eggs as the brood patch developed (Haftorn & Reinertsen 1985), rather than due to an increased requirement of heat to maintain the same egg temperature, as egg temperature increased through the incubation period.



Table 1. Estimates of avian maximal thermogenesis

Species	Mean mass (g)	Reference	Maximum metabolic rate as a multiple of resting or basal metabolic rate*
American Tree-Sparrow <i>Spizella arborea</i>	18.6	Dutenhoffer & Swanson 1996	6.2
Black-Capped Chickadee <i>Parus atricapillus</i>	13.7	Dutenhoffer & Swanson 1996	7.1
Black-Capped Chickadee <i>Parus atricapillus</i>	13.0	Cooper & Swanson 1994	7.5
Black-Capped Chickadee <i>Parus atricapillus</i>	13.1	Cooper & Swanson 1994	6.9
Dark-Eyed Junco <i>Junco hyemalis</i>	20.0	Dutenhoffer & Swanson 1996	6.1
Dark-Eyed Junco <i>Junco hyemalis</i>	17.0	Swanson 1990	7
Downy Woodpecker <i>Picoides pubescens</i>	23.8	Liknes & Swanson 1996	6
Eastern Wood-Pewee <i>Contopus virens</i>	14.0	Dutenhoffer & Swanson 1996	6.5
Evening Grosbeak <i>Coccothraustes vespertinus</i>	62.0	Hart, J.S. 1962	5.6
Field Sparrow <i>Spizella pusilla</i>	12.8	Dutenhoffer & Swanson 1996	6.3
Gray Catbird <i>Dumetella carolinensis</i>	34.4	Dutenhoffer & Swanson 1996	5.6
House Finch <i>Carpodacus mexicanus</i>	23.0	Dawson et al. 1983, Root et al 1991	5.8
House Sparrow <i>Passer domesticus</i>	27.2	Dutenhoffer & Swanson 1996	8.1
House Sparrow <i>Passer domesticus</i>	25.5	Koteja 1986	5.2
House Wren <i>Troglodytes aedon</i>	10.5	Dutenhoffer & Swanson 1996	7.4
Feral Pigeon <i>Columbia livia</i>	404.0	Hart, J.S. 1962	5.0
Rose-Breasted Grosbeak <i>Pheucticus ludovicianus</i>	40.7	Dutenhoffer & Swanson 1996	5.7
Redpoll <i>Carduelis flammea</i>	14.0	Rosenmann & Morrison 1974	5.9
White-Breasted Nuthatch <i>Sitta carolinensis</i>	19.0	Liknes & Swanson 1996	7
Yellow Warbler <i>Dendroica petechia</i>	9.3	Dutenhoffer & Swanson 1996	5.5

\* It was not apparent whether metabolic measurements were post-absorptive in all studies so that specific dynamic action may have contributed to metabolic rate (Ricklefs 1974).

## COSTS OF THERMOREGULATION

Dotterel's energetic costs of thermoregulation were estimated using Wiersma & Piersma's (1994) model for a standing shorebird, based on the power required to maintain the temperature of a taxidermic mount exposed to different weather conditions. Uniparental incubating dotterel spend a mean of 82% of time sitting on their nests, which may increase their rate of heat loss through conduction to the ground and/or reduce their rate of heat loss through passive and forced convection compared with a standing bird (Williams & Dwinell 1990), although wind speed measured with a hand-held anemometer did not significantly differ between 0.09m and 0.02m above ground level in *Racomitrium lanuginosum* heath, paired t-test:  $T_{63}=0.509$ ,  $P=0.612$ ). Additionally, the net thermoregulatory costs when sitting on eggs may be lower than when standing because heat lost from the belly to the clutch is already accounted for in the costs of incubation. The values calculated from Piersma & Wiersma's model are, therefore, an index of the energetic cost of thermoregulation of nesting dotterel, rather than a measure of absolute cost. The coefficients for a lone red knot *Calidris canutus* standing on a tundra hillock were used, as the estimated mean mass of an incubating dotterel (116g, S. Holt et al. unpublished data) is similar to red knot (130g, Wiersma & Piersma 1994) and this most closely matches dotterel's nesting habitat. The mean daily index of the cost of thermoregulation was always greater than the BMR (BMR estimated according to Kersten & Piersma 1986).

## TIPULA MONTANA ABUNDANCE

Adults of the crane fly species *Tipula montana* are relatively large and slow moving and, during the typically 3-week emergence period, very abundant. When available, they form an important part of dotterel's diet (Galbraith et al. 1993). The abundance of adult *T. montana* was measured from transects. Approximately every three days, the observer slowly walked between five and ten 10m transects and counted the number of adult *T. montana* seen in a 2m band centred along each transect. There was no *T. montana* emergence on site B in 1997, a relatively large emergence in 1998 and small emergences on site D in both 1997 and 1998.

Statistical tests were carried out using SPSS (Norusis 1990). Two-tailed probabilities are given. Means are quoted  $\pm$  95% confidence limits or, for non-normally distributed variables, medians  $\pm$  95% confidence limits calculated using Nair's table (Campbell 1989).

## Results

### NEST ATTENDANCE AND ENERGETIC CONSTRAINT

Daily nest attendance at uniparental nests was less when the estimated mean daily cost of steady-state incubation was higher and when the mean daily index of the cost of thermoregulation was higher, and higher during *Tipula montana* emergences (Table 2, Fig. 3). By inserting mean values for the rest of the parameters in the model in Table 2, attendance was estimated to vary by 4.1% over the range of observed values for the index of the cost of thermoregulation and vary by 16.3% over the range of estimated steady-state incubation costs. Daily nest attendance was also lower when the mean costs of steady-state incubation and thermoregulation over the preceding days were higher (Table 3). Attendance also declined through the incubation period (Tables 2 & 3).

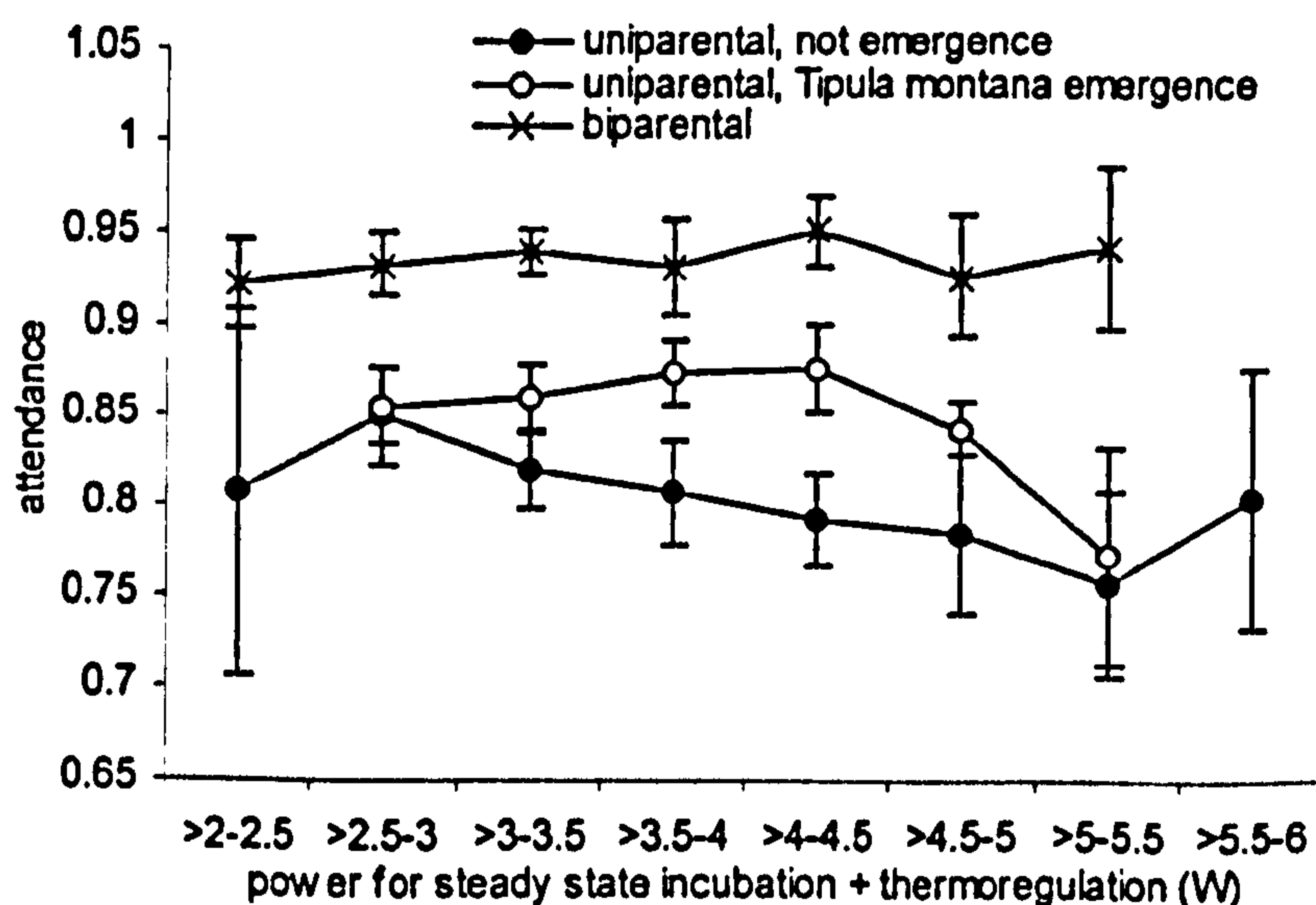


Figure 3. Variation in daily attendance with energetic costs (mean  $\pm$  95% c.l. of between two and 30 nests means for each power category).

Table 2. GLM of the effects of the mean daily costs of steady state incubation and thermoregulation, the availability of adult *Tipula montana* and stage of incubation on the daily proportion of time uniparental nests were attended, controlling for differences between nests by entering a term for nest identity (overall  $R^2_{adj}=0.455$ ). The costs of thermoregulation and steady state incubation and days since clutch initiated were entered as covariates, *T. montana* availability as a fixed factor and nest identity as a random factor.

Daily attendance

factor	<i>F</i>	<i>d.f.</i>	<i>P</i>	Partial $R^2$	$\beta$
Intercept	492.950	1,521.1	<0.001	0.486	
mean cost of thermoregulation during day	5.389	1,507	0.021	0.011	-0.011
mean cost of steady state incubation during day	37.066	1,507	<0.001	0.068	-0.402
adult <i>Tipula montana</i> availability	11.933	1,507	0.001	0.023	-0.040 if unavailable 0 if available
days since clutch initiated	45.457	1,507	<0.001	0.082	-0.003
nest identity	4.960	37,507	<0.001	0.266	

Table 3. GLM as Table 2 but including additional terms for the mean costs of thermoregulation and steady state incubation over the preceding five days (entered as covariates). We also tested similar models that separately included terms for the mean costs over the preceding one, two, three, four, six and seven days. The mean costs of steady state incubation over three, four and six preceding days significantly affected attendance to  $P < 0.05$ . The mean costs of thermoregulation over seven days had significant effects to  $P < 0.05$  and over four and six days to  $P < 0.1$ . We present the minimal model that included terms for mean costs during the preceding five days as this model explained most variation (model  $R^2_{adj} = 0.474$ ). Sample sizes are smaller than in Table 2 as daily attendance data could only be included if incubation had commenced at least five days before.

Daily attendance

Factor	<i>F</i>	<i>d.f.</i>	<i>P</i>	Partial $R^2$	$\beta$
intercept	296.807	1,477.9	<0.001	0.383	1.454
mean cost of thermoregulation during day	6.427	1,470	0.012	0.013	-0.013
mean cost of steady state incubation during day	8.960	1,470	0.003	0.019	-0.240
mean cost of thermoregulation during the preceding five days	10.381	1,470	0.001	0.022	-0.030
mean cost of steady state incubation during the preceding five days	4.012	1,470	0.046	0.008	-0.182
adult <i>Tipula montana</i> availability	10.997	1,470	0.001	0.023	-0.039 if unavailable 0 if available
days since clutch initiated	36.607	1,470	<0.001	0.072	-0.003
nest identity	5.398	35,470	<0.001	0.287	

The sample of only eight biparental nests gave insufficient statistical power to construct models of the influences on nest attendance. However, there was significantly less variation in daily attendance within biparental nests than within uniparental nests, although there was

no difference in variation in the costs of steady-state incubation or thermoregulation between uniparental and biparental nests, suggesting that attendance at biparental nests was less influenced by environmental conditions (independent t-tests of the coefficients of variation of daily attendance within nests logged for at least five days: attendance  $t_{41,0}=5.749$ ,  $P<0.001$ , biparental c.v.  $3.31 \pm 0.82$ , uniparental c.v.  $9.31 \pm 1.87$ ; cost of thermoregulation  $t_{41}=1.167$ ,  $P=0.250$ ; cost of steady-state incubation  $t_{7,9}=1.862$ ,  $P=0.100$ , see also Fig. 3).

#### NEST ATTENDANCE AND BODY RESERVES

Nest attendance (taking nest identity coefficients from the model in Table 3) was positively correlated with a measure of the level of body reserves for the stage of incubation (mass residualised for the stage of incubation and for wing length, as a measure of structural size, Holt et al. 2002, Fig. 4).

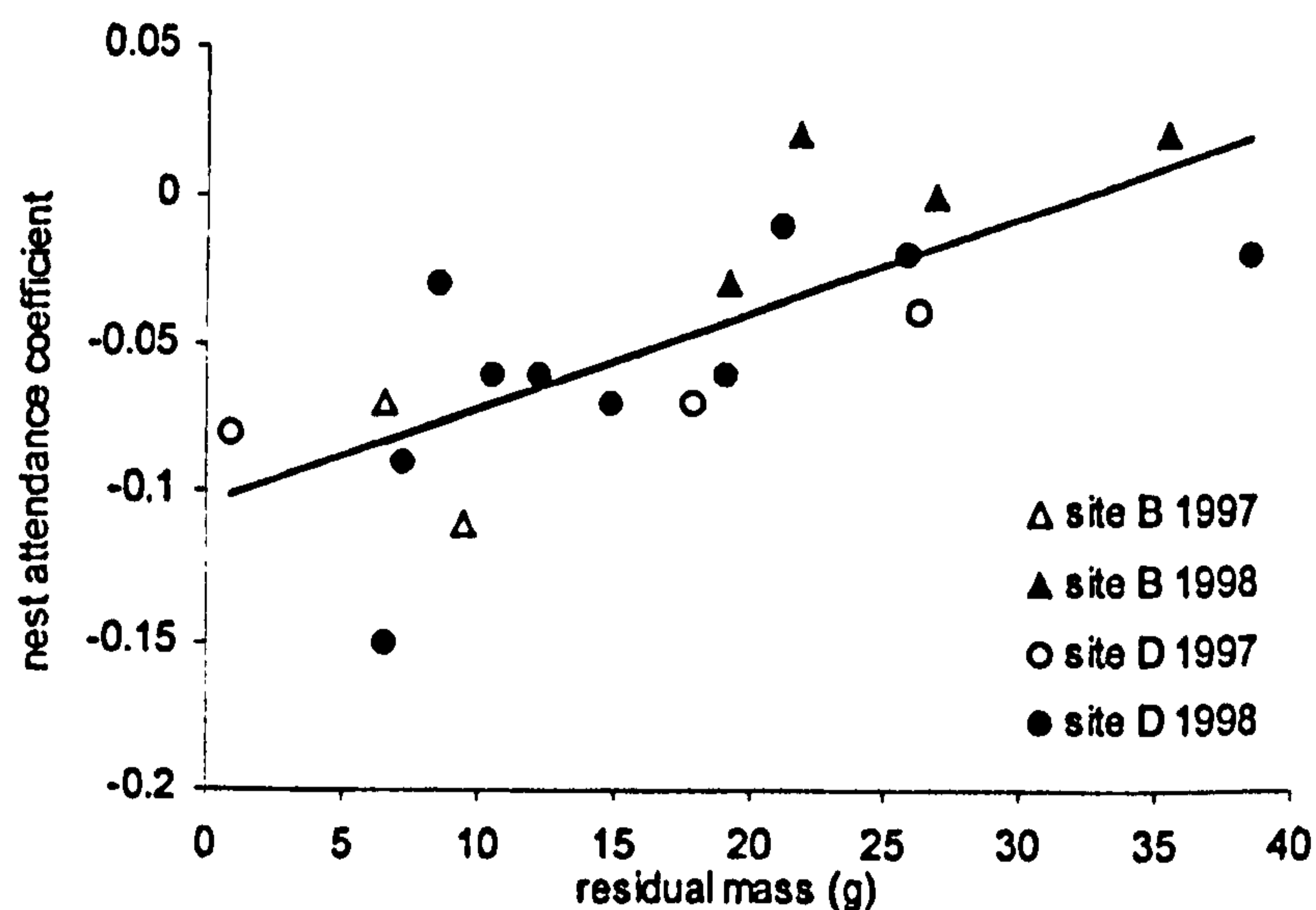


Figure 4. The relationship between attendance (nest identity coefficient from the model in Table 3) and body reserves (mass residualised for wing length and stage of incubation, Holt et al. 2002) at uniparental nests. Nest attendance coefficients and residual mass were significantly, positively correlated (Pearson correlation:  $r=0.740$ ,  $N=19$  nests,  $P<0.001$ ).

## TIME BELOW THE INDEX OF PZT AND ENERGETIC CONSTRAINT

We do not know the PZT for dotterel and PZT is likely to vary between species (Webb 1987). However, the following analyses, which use a value of 20°C as an index of the PZT (Wilson 1991), should reflect relationships between incubation scheduling and dotterel's actual PZT as the proportion of time eggs spent below 20°C was strongly, positively correlated with the proportion of time they spent below all temperatures (tested in 1°C increments) between 15°C and 35°C (Spearman's rank correlation:  $r_s$  between 0.753 and 0.996,  $N=46$  nests and  $P<0.001$  in all tests).

Eggs of biparental nests spent less time below 20°C than those of uniparental nests (t-test:  $t'_{42,1}=6.469$ ,  $P<0.001$ , uniparental clutches spent  $10.8\% \pm 2.6\%$  of time below 20°C,  $N=38$  nests, biparental clutches  $2.0\% \pm 0.8\%$ ,  $N=8$  nests, Fig. 5). However, this analysis may have been confounded as the power for steady-state incubation was significantly higher for uniparental nests than biparental nests, although neither the power for thermoregulation nor egg cooling rate differed (independent t-tests: power for steady-state incubation  $t_{41}=2.279$ ,  $P=0.028$  uniparental  $0.89 \pm 0.02W$ , biparental  $0.83 \pm 0.04W$ ; power for thermoregulation  $t_{41}=0.790$ ,  $P=0.434$ ; egg cooling rate  $t_{41}=0.524$ ,  $P=0.603$ ). To avoid the potentially confounding effect of different costs of steady-state incubation, a small sample of pairs of uniparental and biparental dotterel incubating at the same time on the same site were compared: the eggs of biparental nests were again found to spend less time below 20°C than those of uniparental nests (paired t-test:  $T_5=2.662$ ,  $P=0.045$ , uniparental clutches spent  $8.5\% \pm 6.3\%$  more time below 20°C than biparental clutches, pairs compared between 9.6 and 18.3 days per pair of nests).

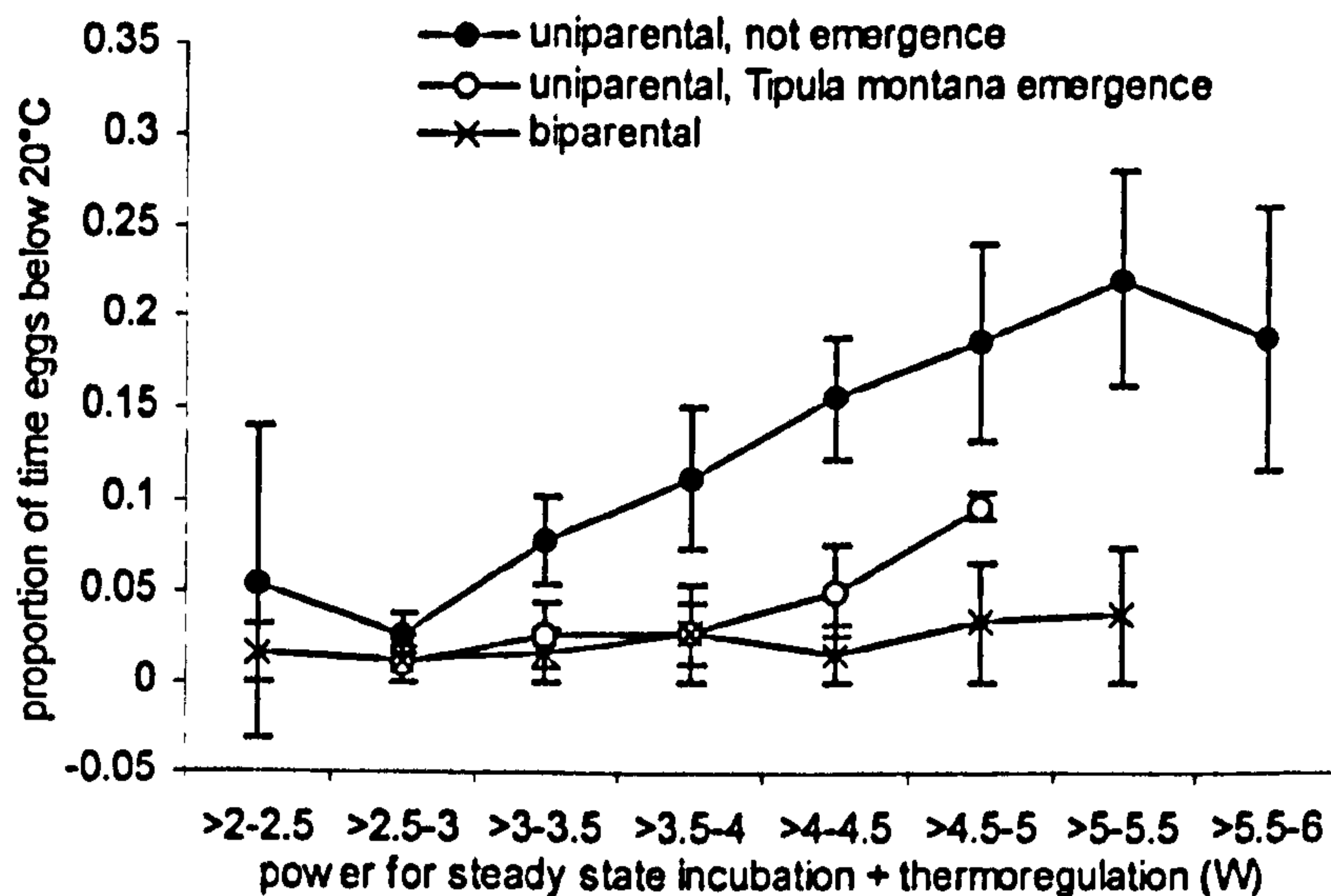


Figure 5. The daily proportion of time (mean  $\pm$  95% c.i.) that eggs spent below 20°C with daily energetic costs, parental care system and adult *Tipula montana* availability (during *T. montana* emergences 2 to 9 uniparental nest means were used to calculate each power class mean, not during emergences 7 to 30 uniparental nests and between 5 to 8 nest means were used for biparental means).

Within uniparental nests, the eggs spent significantly less time below 20°C during *Tipula montana* emergences (paired t-test:  $t_{11}=3.201$ ,  $P=0.008$ , eggs spent 5%  $\pm$  3% less time below 20°C during emergences, using only nests with at least two days logged with both *T. montana* available and *T. montana* unavailable). This result was not due to differing conditions as there was no significant difference in the power for thermoregulation or steady-state incubation or in egg cooling rate within nests when compared in the presence and absence of a *T. montana* emergence (paired t-tests: power for thermoregulation  $t_{11}=1.758$ ,  $P=0.106$ ; power for steady-state incubation  $t_{11}=1.657$ ,  $P=0.126$ ; egg cooling rate  $t_{11}=1.118$ ,  $P=0.287$ ).

Within uniparental nests, when adult *T. montana* were not available, eggs spent significantly more time below 20°C in poor conditions than in good conditions (paired t-test:  $t_{15}=7.391$ ,  $P<0.001$ , eggs spent 17%  $\pm$  5% more time below 20°C in poor conditions, Fig. 5). Good conditions were when the combined power for thermoregulation and steady-state incubation for both that day and the mean value over the preceding five days were less than the overall



mean combined power of 3.84W and poor conditions were when both the one day and five day power values exceeded the mean. The test used only nests with at least two days logged in each condition category.

#### ENERGETIC CONSTRAINT AND ENERGY EXPENDED ON INCUBATION

There was no significant difference between the nest-means of the daily cost of incubation between uniparental and biparental nests ( $t_{41}=1.767$ ,  $P=0.085$ , mean daily power for incubation for uniparental nests  $0.98 \pm 0.03W$ , biparental nests  $0.92 \pm 0.05W$ , using nests with at least five logged days). However, this analysis may have been confounded as the power for steady-state incubation was significantly higher for uniparental nests than biparental nests, although neither the power for thermoregulation nor egg cooling rate differed (see the tests of time spent below 20°C with parental care for statistics). To avoid the confounding effect of the different costs of steady-state incubation the estimated cost of incubation was compared within a small sample of pairs of uniparental and parental nests incubating at the same time on the same site: the cost was again found not to differ between parental care systems (paired t-test:  $T_5=0.534$ ,  $P=0.616$ ,  $0.03 \pm 0.12W$  or  $4.3\% \pm 12.7\%$  more power expended at uniparental nests, pairs compared between 9.6 and 18.3 days). Attendance was significantly higher at biparental nests than uniparental nests (Chapter 4) and, in the larger, unmatched sample, trip length and the rate of trips from the nest were significantly lower for biparental nests (independent t-tests: median trip length,  $t_{44}=2.122$ ,  $P=0.040$ , uniparental nests  $9.4 \pm 0.9$  min, biparental  $7.2 \pm 1.2$ ; trip rate,  $t_{41}=4.013$ ,  $P<0.001$ , uniparental  $0.70 \pm 0.18$  hr<sup>-1</sup>, biparental  $0.39 \pm 0.11$  hr<sup>-1</sup>).

Uniparental dotterel did not expend significantly more energy on incubation when food was more abundant during *Tipula montana* emergences (paired t-test comparing the mean of the daily power for incubation for the same nests during *T. montana* emergences and when *T. montana* was unavailable:  $t_{11}=1.444$ ,  $P=0.177$ , tests comparing mean daily values were confined to nests with at least two logged days with and without *T. montana*, power for incubation was  $0.03 \pm 0.04W$ , or  $3.5 \pm 4.2\%$ , greater during emergences). This lack of

difference was not a consequence of other conditions varying between *T. montana* emergences and when *T. montana* were not available (see the effect of emergence on time below the 20°C for statistics). During an emergence, trip rate and attendance were significantly greater while trip length and, consequently, the proportion of the potential temperature drop to equilibration that eggs underwent during trips, were significantly less (paired t-tests: trip rate  $t_{11}=2.982$ ,  $P=0.012$ ,  $0.21\text{hr}^{-1} \pm 0.14\text{hr}^{-1}$  or  $35\% \pm 22\%$  greater during emergences; attendance  $t_{11}=3.154$ ,  $P=0.009$ ,  $0.04 \pm 0.02$  or  $4\% \pm 3\%$  greater during emergences; proportion of potential temperature drop  $t_{13}=4.092$ ,  $P=0.001$ ,  $0.07 \pm 0.03$  or  $13\% \pm 7\%$  less during emergences; Wilcoxon signed ranks test: median trip length  $z=3.071$ ,  $N=14$ ,  $P=0.002$ , trips were a median of  $1.8 \pm 0.9$  to  $2.9$  min or  $23\% \pm 10\%$  to  $31\%$  shorter during emergences).

When adult *T. montana* were not available, uniparental dotterel used significantly more power for incubation in good conditions than in poor conditions (paired t-test comparing the mean daily power for incubation in good conditions with the mean daily power for incubation for the same nests in poor conditions:  $t_{15}=5.166$ ,  $P<0.001$ , power for incubation was  $0.15 \pm 0.06\text{W}$  or  $17.7\% \pm 7.3\%$  greater in good conditions). This analysis oversimplifies the overall pattern of variation in power used for incubation with conditions as, in very good conditions, the power expended on incubation appeared to reduce (Figs. 6 and 7b). However, by chance, the sample analysed above contained no days when the combined power for steady-state incubation and thermoregulation were less than 3W, when the power expended on incubation appeared to decrease (Fig. 7b). In good conditions attendance and trip rate significantly increased while trip length significantly shortened (paired t-tests for nests where at least two logged days in each category: attendance  $t_{15}=3.890$ ,  $P=0.001$ ,  $0.087 \pm 0.044$  or  $12.9\% \pm 7.1\%$  greater in good conditions; trip rate  $t_{15}=7.757$ ,  $P<0.001$ ,  $0.479\text{hr}^{-1} \pm 0.121 \text{hr}^{-1}$  or  $130.4\% \pm 37.0\%$  greater in good conditions; Wilcoxon signed ranks test, median trip length for nests with at least ten trips in each category  $z=3.697$ ,  $N=26$ ,  $P<0.001$ ,  $2.5 \pm 0.9$  to  $5.3$  mins or  $28.8\% \pm 8.7$  to  $36.7\%$  shorter in good conditions).

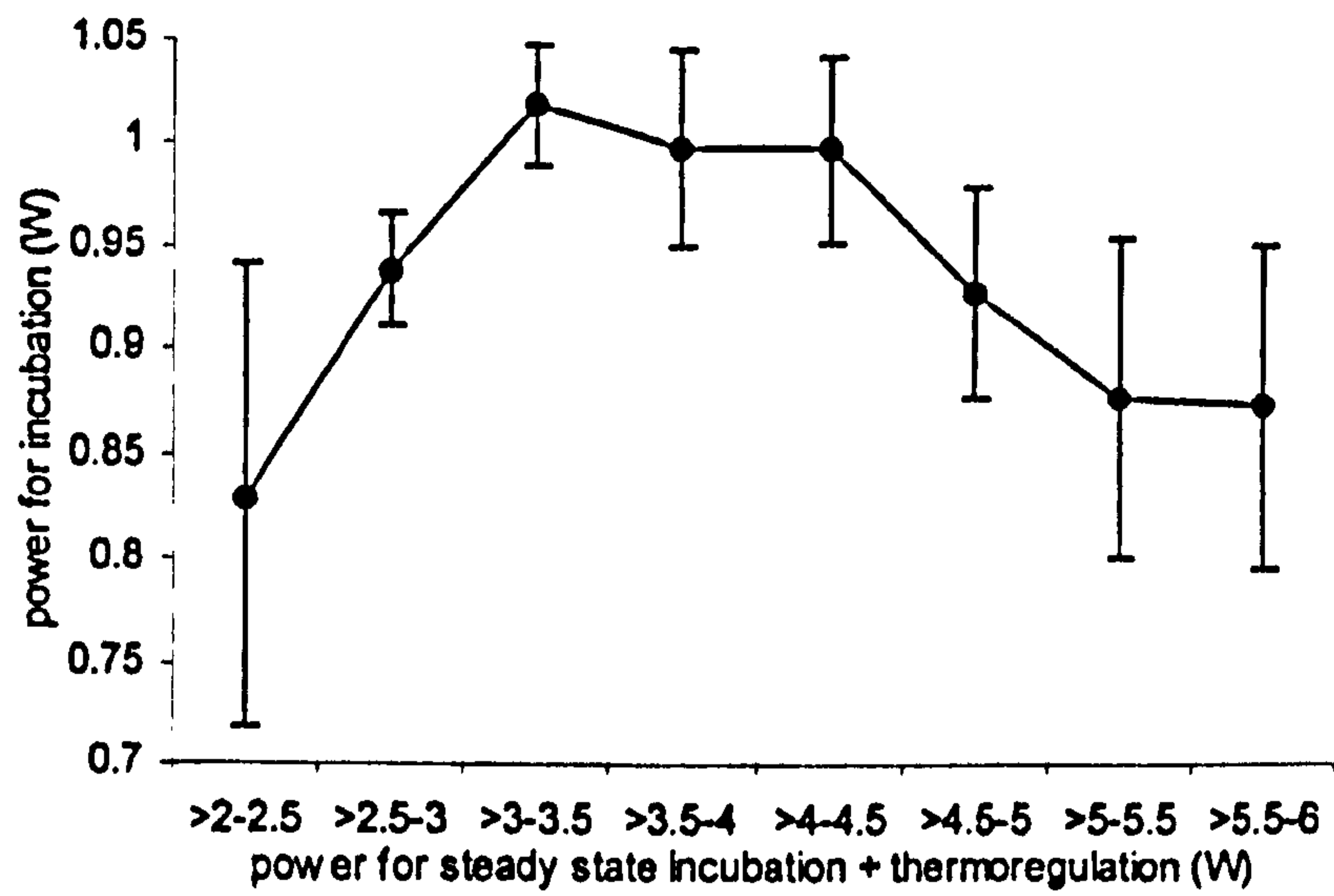


Figure 6. Variation in mean daily power used for incubation with potential power requirements, by uniparental dotterel when adult *Tipula montana* were not available (mean  $\pm$  95% c.i. of seven to 30 nest means in each power category).

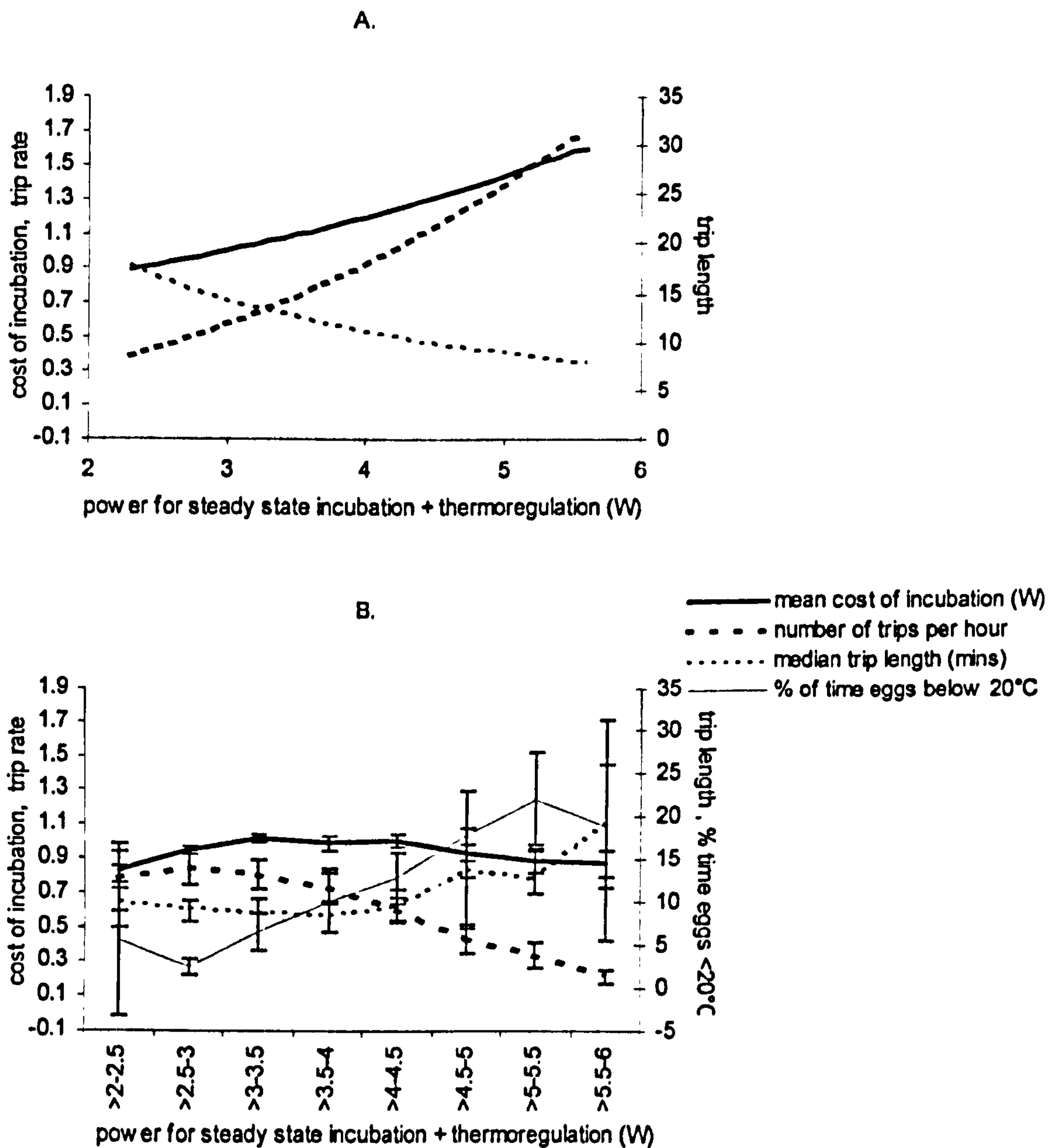


Figure 7. Figure 7a shows the variation in the predicted cost of incubation, trip rate and trip length, if incubation was scheduled to give the least energetically costly incubation that ensured that eggs never cooled below 20°C (i.e. using the trip length at the end of which the eggs cooled to 20°C). Attendance was predicted from power using the model in Table 2. Egg cooling rates increased with the power for steady state incubation and thermoregulation so were calculated from the significant regressions between mean daily power and the mean daily egg cooling coefficients and air temperature during trips (the effect of insolation on egg cooling rate was independent of power so the overall mean value was used) Trips were assumed to be equally spaced in time. Figure 7b shows how the mean daily cost of incubation, trip rate, trip length and proportion of time eggs spent below 20°C actually varied with the combined powers for steady state incubation and thermoregulation at uniparental nests (mean or median  $\pm$  95% c.i. of nest means or medians for between 7 and 35 nests per power class).

## INCUBATION SCHEDULING AND PREDATION RISK

Predator assemblages differed between the two sites: avian egg-predators, which hunt during daylight, were more abundant on site B than site D ( $1.2 \pm 0.1$  groups per day on site B and  $0.1 \pm 0.1$  on site D, 96% of sightings of avian egg-predators were ravens *Corvus corax*) while mammalian predators were probably more important on site D than site B. On site B no dotterel nests were thought to be depredated by mammals but on site D at least six dotterel nests depredated during or close to dark and hence probably by mammalian predators and the remains of several ptarmigan *Lagopus mutus* clutches suggested predation by mustelids (criteria for identification in Bang & Dahlstrøm 1990).

Dotterel made a smaller proportion of trips on and off the nest between sunset to sunrise on site D than on site B (using one value per nest for darkness and for daylight, GLM: light\*site  $F_{1,72}=4.149$ ,  $P=0.045$ , light  $F_{1,1}=0.198$ ,  $P=0.733$ , site  $F_{1,1}=0.193$ ,  $P=0.773$ , darkness was defined as between sunset and sunrise, Fig. 8). This difference was not due to dotterel responding to variation in egg cooling rate as this did not vary with an interaction term between site and light (GLM: light\*site  $F_{1,72}=0.054$ ,  $P=0.816$ , light  $F_{1,1}=553.099$ ,  $P=0.027$ , site  $F_{1,1}=33.686$ ,  $P=0.109$ ).

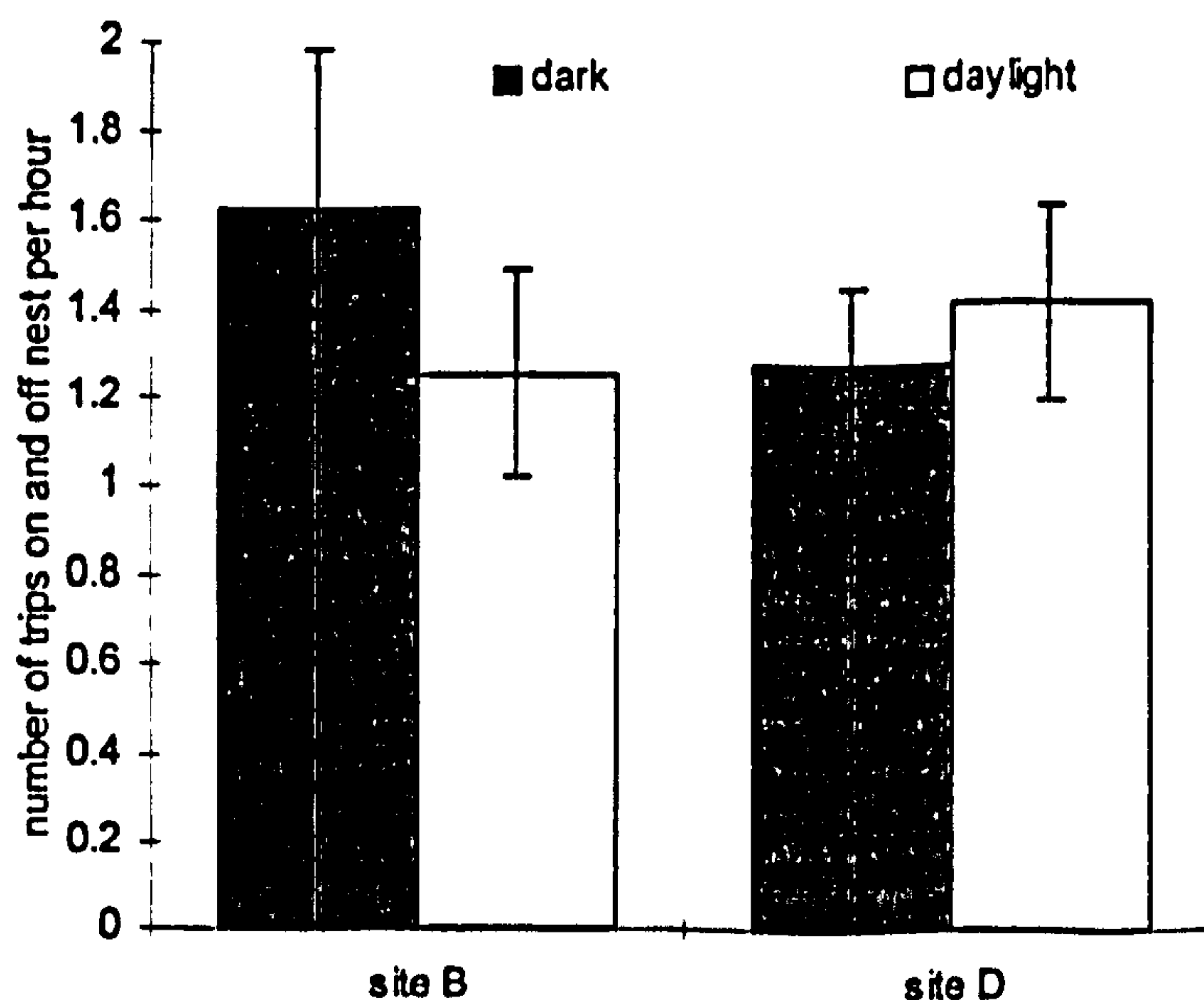


Figure 8. Differences between sites in the rate at which dotterel went on and off the nest between daylight and darkness (means  $\pm$  95% c.i.).

## INCUBATION SCHEDULING AND STAGE OF INCUBATION

The estimated percentage of time that eggs spent below 20°C increased significantly with days since first egg date at uniparental nests (GLM: days since first egg date  $F_{1,421}=17.283$ ,  $P<0.001$ , partial  $R^2=0.039$ ,  $\beta=0.373$ , nest identity  $F_{32,421}=4.695$ ,  $P<0.001$ , partial  $R^2=0.263$ , model  $R^2_{\text{adj}}=0.233$ ). The sample was confined to days from first egg date whose values were estimated from at least four nests but the test remained poorly balanced with  $49\% \pm 6\%$  of 33 nests contributing a datum to each day since first egg date. Variation in the percentage of time that eggs spent below 20°C in was not due to variation in conditions as any days during *T. montana* emergences were excluded and the combined powers for steady-state incubation and thermoregulation did not vary with days since first egg date in the same sample (GLM: days since first egg date  $F_{1,421}=0.077$ ,  $P=0.782$ , partial  $R^2=0.000$ ,  $\beta=0.002$ , nest identity  $F_{32,421}=1.831$ ,  $P=0.004$ , partial  $R^2=0.122$ , model  $R^2_{\text{adj}}=0.056$ ).

## INCUBATION SCHEDULING AND EGG COOLING RATES

Uniparental dotterel appeared to schedule their trips to coincide with conditions when their eggs would have cooled more slowly if unattended, as the potential egg cooling rate of an unattended clutch (the estimated egg temperature drop during the first 5s of inattendance) was significantly lower during trips than while the eggs were attended, whether the whole day or just daylight was considered. During darkness, there was no significant difference in the potential unattended egg cooling rate between trips and periods of attendance (t-test of whether the mean value of daily potential egg cooling rates while attended minus egg cooling rates while unattended differed from 0: whole day,  $t_{37}=8.053$ ,  $P<0.001$ , cooling rate was  $0.0076 \pm 0.0018^\circ\text{C}$  or  $4.0\% \pm 1.1\%$  less during trips; daylight,  $t_{37}=10.746$ ,  $P<0.001$ , cooling rate was  $0.0088 \pm 0.0016^\circ\text{C}$  or  $5.0\% \pm 1.0\%$  less during trips; darkness,  $t_{37}=0.241$ ,  $P=0.881$ , cooling rate was  $0.0004 \pm 0.0036^\circ\text{C}$  or  $1.4\% \pm 5.6\%$  greater during trips).

Over the whole day, if uniparental dotterel's trip scheduling was constrained only by their daily attendance, the best improvement in the potential cooling rate they could have achieved during trips was  $28.0\% \pm 1.2\%$  (calculated from the maximum possible difference in cooling

rate for each nest's daily nest attendance if dotterel were able schedule all their time off the nest to coincide with the lowest cooling rates for the day).

During daylight, mean hourly uniparental nest attendance was closely positively correlated with the mean potential cooling rate but, during darkness, was negatively correlated (Pearson correlation between hourly means of egg cooling rate and nest attendance calculated from 38 nest means: during daylight  $r=0.961$ ,  $N=19$ ,  $P<0.001$ ; during darkness  $r=-0.910$ ,  $N=6$ ,  $P=0.012$ , Fig. 9).

There was no significant difference in the daily mean potential egg cooling rate while biparental nests were attended or unattended over the whole day, during daylight, or during darkness (whole day:  $t_7=0.667$ ,  $P=0.526$ , cooling rate  $0.0014 \pm 0.0043^\circ\text{C}$  or  $0.5\% \pm 2.8\%$  less during trips; during daylight  $t_7=1.683$ ,  $P=0.136$ ,  $0.0036 \pm 0.0042^\circ\text{C}$  or cooling rate  $2.1\% \pm 3.0\%$  less during trips; during darkness  $t_7=0.746$ ,  $P=0.480$ , cooling rate  $0.0017 \pm 0.0044^\circ\text{C}$  or  $0.4\% \pm 2.5\%$  less during trips). The sample size of biparental nests was smaller giving less statistical power to detect trip scheduling than for uniparental nests but uniparental parents did schedule trips to occur in better conditions than biparental parents as, over the whole day, the mean difference in the potential cooling rate between when nests were attended and unattended was significantly greater for uniparental than biparental nests (t-test:  $t_{44}=2.684$ ,  $P=0.010$ ) even though biparental nests had significantly greater scope for selecting better cooling rates (t-test:  $t_{43}=2.222$ ,  $P=0.032$ , mean best potential difference in cooling rate for uniparental nests  $0.0488 \pm 0.0017^\circ\text{C}$ , biparental nests  $0.0531 \pm 0.0028^\circ\text{C}$ ).

While the pattern of nest attendance during darkness did not appear to minimise the egg cooling rate during trips, similar patterns were observed in uniparental and biparental nests (Pearson correlation of mean hourly nest attendance calculated from eight biparental and 38 uniparental nests:  $r=0.983$ ,  $N=6$ ,  $P<0.001$ ).

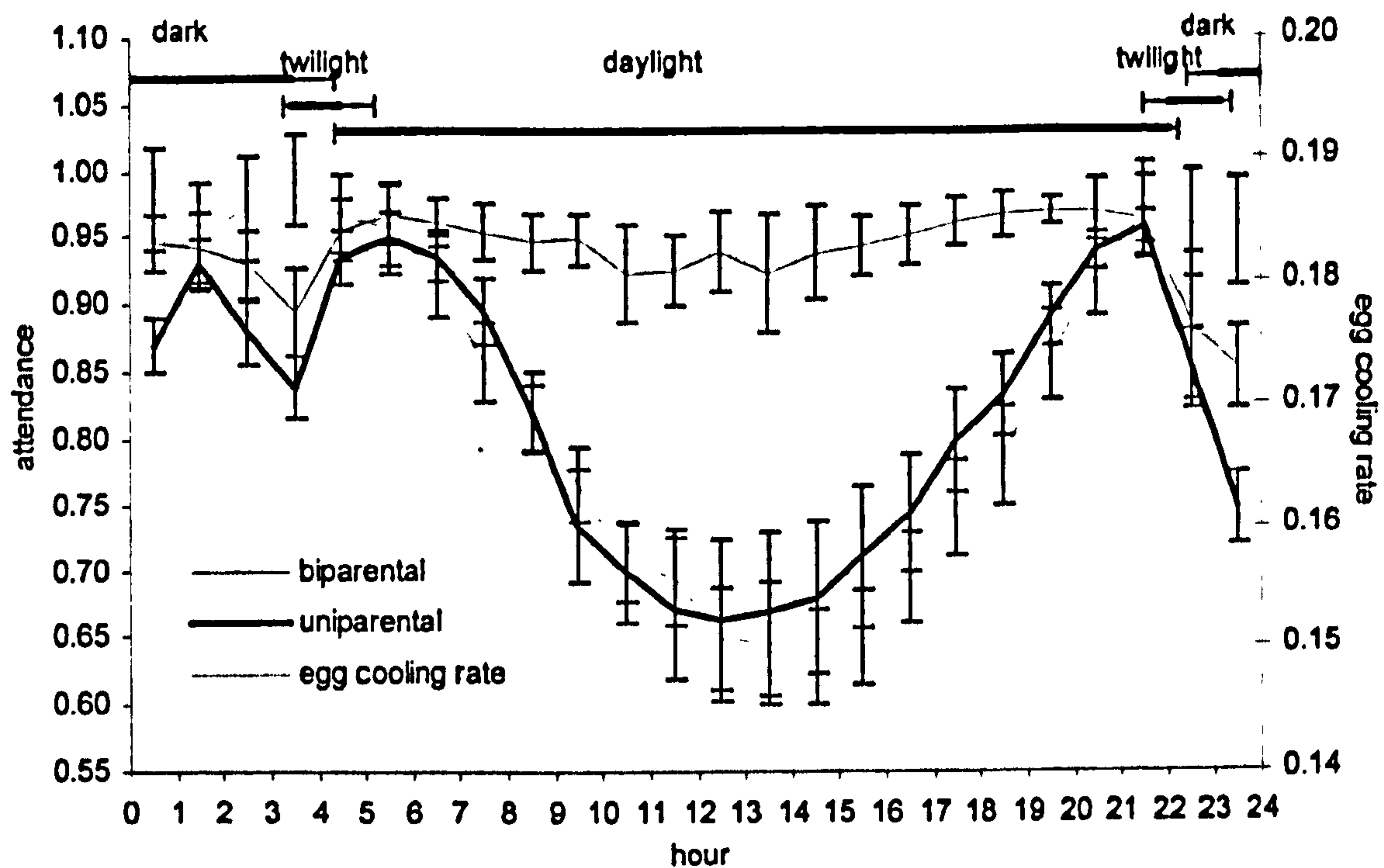


Figure 9. Variation in nest attendance and egg cooling rate through the day (mean  $\pm$  95% c.i., British Summer Time). The top bars indicate the mean and range of times of daylight, twilight and darkness while dotterel were incubating.

## Discussion

### WERE DOTTEREL ENERGETICALLY CONSTRAINED DURING INCUBATION?

Attendance at uniparental nests appeared to be constrained by the balance between energetic costs and food intake because attendance decreased when the current and past energetic costs of steady-state incubation and thermoregulation were higher, and increased when the important prey *Tipula montana* was available. For biparental nests, where the costs of incubation are shared between two individuals that have more off-duty time in which to forage, attendance did not appear to vary with energetic costs. As might be expected from the pattern of attendance, the proportion of time that eggs spent below 20°C was constrained by the same balance between energetic costs and food intake: within uniparental nests, the proportion of time eggs spent below 20°C decreased when *T. montana* was available and when energetic costs were lower, and the eggs of biparental nests spent less time below



20°C. When more energetically constrained, either because of higher energetic costs or reduced food availability, dotterel reduced nest attendance and allowed the amount of time the eggs spent below 20°C to increase, moving the balance of allocation of time away from maintaining the embryos' current thermal environment towards care of self. When overall energetic costs were lower, uniparental dotterel achieved the decrease in time eggs spent below 20°C by increasing their energetic expenditure on incubation. To schedule incubation, for a given level of nest attendance, so that the eggs are never allowed to cool below the 20°C index of PZT (as temperate passerines generally appear to, Haftorn 1988), dotterel would have to decrease trip length as conditions worsened, increasing trip frequency and the cost of incubation (Fig. 7a). This increase in costs is exacerbated since the same poor conditions mean that dotterel must reduce nest attendance to spend more time foraging, and lower nest attendance carries higher costs of incubation for most trip durations (Fig. 10). Dotterel appeared to increase expenditure on incubation as conditions deteriorate from good to moderate but decrease expenditure as conditions worsen by increasing trip length and reducing trip rate, with the consequence that the eggs spend more time below 20°C.

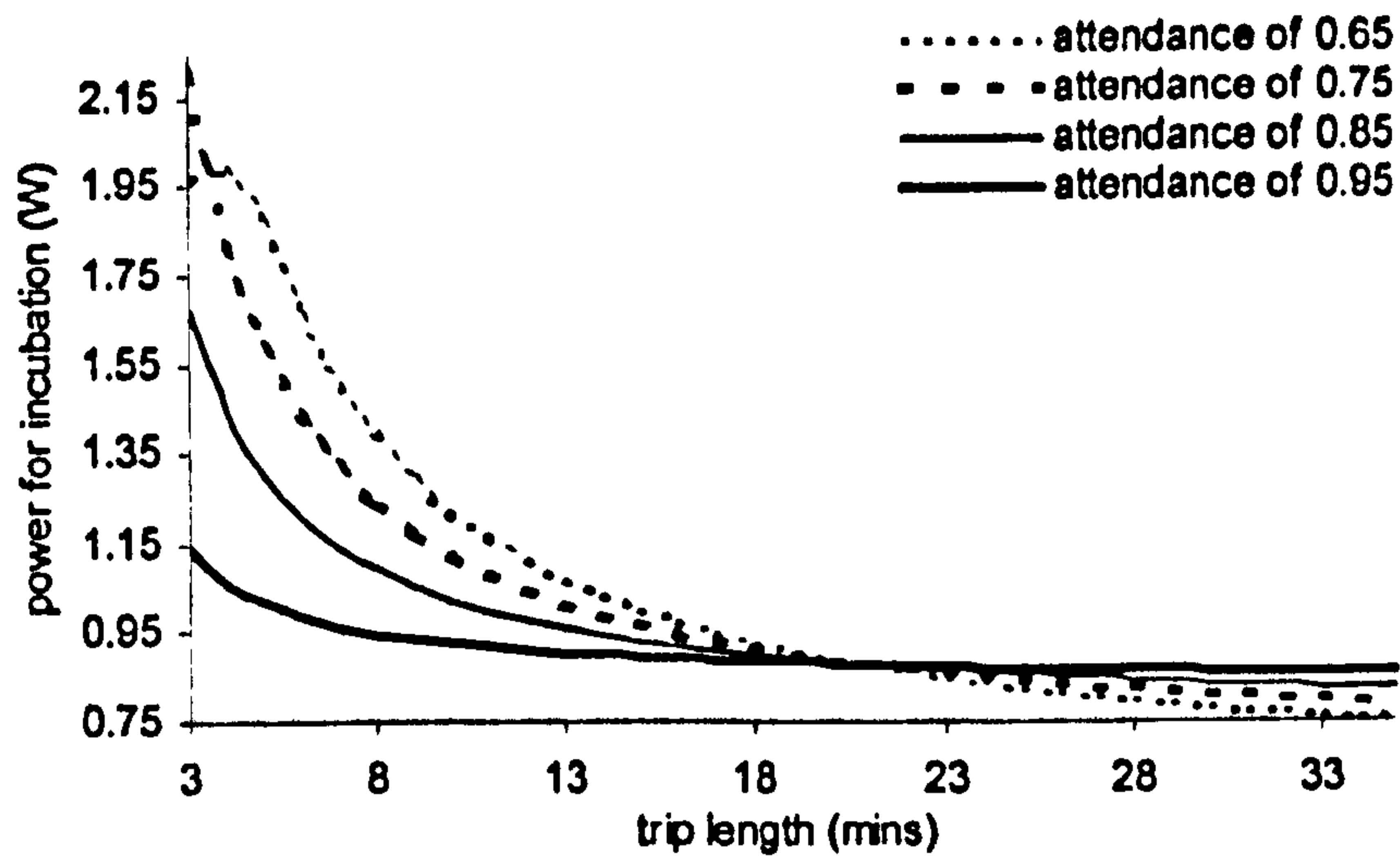


Figure 10. Model of variation in the power for incubation with trip length and attendance (estimated using mean egg cooling rate during trips and mean ground temperature). The figure covers 90% of the observed range of values of trip length and attendance. Under average conditions, the cost of incubation declines with increasing trip length and, below a trip length of 22 mins (which includes  $90\% \pm 2\%$  of trips from the 38 uniparental nests and  $94\% \pm 2\%$  from the eight biparental nests) the power for incubation declines with increasing nest attendance. The model assumes that trips are equally spaced in time so that power for incubation declines for very short trips at low attendance, when the eggs are never fully rewarmed to the optimum temperature.

#### WHY DID DOTTEREL APPEAR TO CAP THEIR ENERGETIC EXPENDITURE ON INCUBATION?

The potential costs of incubation and the cost of thermoregulation increase together in poorer weather (Haftorn 1988 & references therein; Thomson et al. 1998b) and expenditure on incubation may be capped if dotterel reach their maximal thermogenesis (Weiner 1992) or their maximum sustainable work load (Drent & Daan 1980), although there is some doubt that maximum sustainable work load universally lies around Drent & Daan's 4 x BMR (Bryant 1988; Bryant & Tatner 1991; Piersma & Morrison 1994). Alternatively, dotterel may be operating below their ceiling of thermogenesis or sustainable work but limiting their expenditure on incubation to balance their energy budget. Similarly, some bird species increase energetic expenditure on incubation with clutch size or declining egg temperature up to a plateau, beyond which they may be unable or unwilling to increase expenditure further

(Mertens 1977; Tøien 1989; Moreno & Sanz 1994): in chickens *Gallus domesticus* this limit probably corresponds to their maximal thermogenesis (Williams 1996).

#### ENERGETIC EXPENDITURE AND THE DEGREE OF ENERGETIC CONSTRAINT

Contrary to our second prediction, dotterel did not always respond to changes in their degree of energetic constraint by altering their energetic expenditure on incubation: expenditure on incubation was higher for neither uniparental nests when food was more abundant nor for biparental nests. At biparental nests two parents share the costs of incubation and have more off-duty time in which to forage (Holt et al. 2002), so that their energetic expenditure will be less constrained. Although two parents provided a better thermal environment for their eggs than lone parents, they did so without expending more energy as a pair. Biparental parents were able to increase attendance with an unchanged trip length, so reducing egg rewarming costs and the overall costs of incubation (Fig. 10). Similarly, although uniparental dotterel's energetic expenditure is probably less constrained during *Tipula montana* emergences, they did not increase the energy used for incubation while they improved their eggs' thermal environment. The increased food abundance presumably increased dotterel's foraging efficiency, which allowed them to spend less time feeding and more time on the nest. The rate of energy expenditure of shorebirds nesting in the arctic may be higher while off the nest than while on the nest (Tulp et al. 1998) so that the decrease in foraging time due to increased foraging efficiency may also reduce the foraging component of daily energy expenditure without reducing food intake. During emergences of *T. montana*, dotterel increased their rate of making trips but the shorter trips and consequently smaller drop in egg temperature must have at least partially compensated for the increased cost of more frequent rewarming.

Although less energetically constrained, neither biparental dotterel nor uniparental dotterel during *T. montana* emergences increased their energy expenditure on incubation, although they did improve their eggs' thermal environment. In both cases, some of the 'spare' energy appeared to be channelled into increasing or maintaining body reserves as both uniparental dotterel during emergences and biparental dotterel had greater body masses after controlling for the effects of structural size, site and stage of breeding (Holt et al. 2002).

In summary, the balance of dotterel's allocation of time and energy between maintaining a suitable thermal environment for the eggs and maintaining their own energy budget and body reserves depended on the degree of energetic constraint they experienced. In poor weather conditions, which increased their thermostatic energetic demands, uniparental dotterel reduced their energetic investment in incubation, worsening their eggs' thermal environment. When less energetically constrained, either when sharing incubation or when food was abundant, dotterel improved their eggs' thermal environment but without increasing their expenditure on incubation, apparently channelling 'spare' energy into body reserves.

#### SUPPLEMENTATION OF THE ENERGY BUDGET USING BODY RESERVES

Incubating dotterel supplement their energy budget using body reserves so that reserves decline through the incubation period (Kálás & Byrkjedal 1984; Pulliainen & Saari 1992; Holt et al. 2002). Nest attendance also declined through the incubation period and the estimated proportion of time that eggs spent below the index of PZT consequently increased. Energetic costs did not change through the incubation period and the lack of any effect of nest initiation date suggests that the decline in attendance was not a seasonal effect. The decline in attendance is also unlikely to be a consequence of the increased thermogenesis of older embryos, resulting in an enhanced thermal environment, as the increase in eggs' thermal conductance through greater embryonic circulation is likely to counter any such effect and embryonic metabolic rate may contribute little at the low ambient temperatures while unattended (Khaskin 1961; Turner 1991; Mathiu et al. 1994; Turner 1994c; Williams 1996).

As in other species (reviewed in Reed et al. 1995), decreasing nest attendance through the incubation period by uniparental dotterel may reflect a reduction in the ability to supplement their energy budgets using stored body reserves as they were depleted towards hatch. Supporting this, uniparental dotterel with greater body reserves for their stage of incubation attended more, although this may be because both reserves and attendance vary with the net energy budget without any direct causal relationship between them. However, Kálás & Løfaldli (1987) found that dotterel reduced nest attendance when their masses were

experimentally decreased by increasing clutch size. Similarly, Canada geese *Branta canadensis* that started incubation with greater body reserves had higher nest attendance (Aldrich & Raveling 1983) and barn swallows *Hirundo rustica* and willow grouse *Lagopus lagopus* with low masses spent less time incubating (Erikstad 1986; Jones 1987). Nest attendance declined in uniparental dotterel when the energetic costs of thermoregulation and incubation over the preceding five days were higher (presumably causing more body reserves to be utilised to supplement the energy budget), providing further evidence that reduced body reserves constrained attendance.

#### DO INCREASES IN THE ENERGETIC COSTS OF INCUBATION TRANSLATE INTO INCREASED DAILY ENERGY EXPENDITURE?

An increased cost of incubation may result in increased daily energy expenditure (DEE, Moreno et al. 1991; Moreno & Sanz 1994). However, variation in the costs of incubation may not directly translate into variation in DEE if there is behavioural compensation (i.e. when incubation is energetically expensive, birds may behaviourally reduce the cost of other activities), if the factors that increase the cost of incubation decrease other energetic costs or if heat produced from locomotion or physiological processes contributed much of the heat required for incubation.

The main residual elements of an incubating dotterel's energy budget are thermoregulation, which typically makes up 40-60% of a bird's energy expenditure (Bakken 1990), foraging, including locomotion, anti-predator behaviours and moult (Walsberg 1983), although moult will only be a cost for later nesting birds (D.P. Whitfield unpublished data). Overall, there seems to be little scope for the costs of other activities to decrease due to variation in the factors that increase the costs of incubation. The energetic cost of thermoregulation is higher in the weather conditions that increase the rates of heat loss from both attended and unattended eggs, potentially increasing the cost of incubation (Haftorn 1988 & references therein; Thomson et al. 1998b).

But could a dotterel's behaviour reduce these other costs to compensate for an increased cost of incubation? Once a dotterel has selected a nest site, it can do little more than adjust its posture and orientation to influence its cost of thermoregulation while sitting. Otherwise, dotterel could probably only vary their cost of thermoregulation by spending more time off the nest in favourable microhabitats but this was unlikely because dotterel usually foraged intensively in exposed habitats during trips (Galbraith et al. 1993; pers. obs). It appeared that, rather than compensating for an increased cost of incubation by decreasing the apparently obligate cost of thermoregulation, uniparental dotterel changed their incubation scheduling to reduce their more elective energy expenditure on incubation, to compensate for an increased cost of thermoregulation (whereas the less energetically constrained biparental dotterel were able to increase expenditure on incubation when thermoregulatory costs increased, S. Holt et al, unpublished data). Dotterel also decreased their nest attendance when the cost of steady-state incubation (a measure of the potential cost of incubation) was higher: dotterel appeared to compensate for an increased potential cost of incubation by changing their incubation scheduling.

It is unlikely that dotterel can use substantially less energy while foraging to compensate for higher incubation costs since single parents are expected to maximise net energy gain rate in order to minimise the time spent off the nest. Overall energy expended on foraging may even increase under the weather conditions that increase incubation costs because prey may be less available (MacLean & Pitelka 1971). There may have been some compensation in anti-predation behaviours as dotterel moved towards a less energetically costly nest defence strategy in colder conditions when incubation would be more costly (Chapter 7). We do not know whether more energetically constrained dotterel retarded moult, as other species may (Lessells 1986).

Substitution of by-product heat from physiological processes and locomotion may have defrayed some of the cost of incubation and thermoregulation (Bruinzeel & Piersma 1998), especially of egg rewarming after a period of inattendance (Biebach 1986). However, although birds may dump stored body heat to help to rewarm eggs, they must also have to

Increase thermogenesis as metabolic rate or breathing rate increases during rewarming (Norton 1973; Cartar & Montgomerie 1985; Biebach 1986; Biebach 1979 cited in Jones 1987; Tøien 1989; Haftorn & Reinertsen 1990; Turner 1997). The cost of incubation and index of the cost of thermoregulation together averaged  $3.8 \pm 0.1$  times BMR in dotterel (BMR estimated according to Kersten & Piersma 1986), so that substitution can only have been partial.

Although there was probably little scope for energy saving from substitution or costs that were inversely related to the cost of incubation, behavioural compensation through incubation scheduling and, probably less importantly, changes in anti-predation behaviour probably partly compensated for increased potential incubation costs, so that increases in the potential cost of incubation may not have resulted in increases in DEE in uniparental dotterel. However, the less energetically constrained biparental dotterel did not appear to compensate for increased costs of incubation and thermoregulation through their incubation scheduling and increases in the potential cost of incubation may have translated into an increased DEE. The compensatory behaviours that mask any direct fitness consequences of a potential cost may themselves reduce productivity or survivorship, and an increased potential cost of incubation may have fitness consequences even though it may not always result in an increased DEE. Uniparental dotterel reduced nest attendance when the potential costs of incubation were higher, and nests that were attended less took longer to hatch (Chapter 4), which may decrease hatching success (e.g. Tombre & Erikstad 1996): thus the costs of incubation may influence LRS.

#### VARIATION IN THE PATTERN OF ATTENDANCE WITH ENVIRONMENTAL CONDITIONS

Studies describe two different patterns of nest attendance in relation to temperature: in some species, like dotterel, nest attendance increases in better weather conditions or in experimentally warmed conditions (Norton 1972; Vleck 1981b; Sanz 1995 & references therein; Bryan & Bryant 1999; Reid et al. 1999), while in others attendance declines when ambient or egg temperature increases (Green et al. 1990; Eichholz & Sedinger 1999) , although at very high temperatures some species may be compelled to increase nest attendance to prevent damage to their embryos (Drent et al. 1970; Drent 1970; Norton 1972;

White & Kinney 1974; Drent 1975; Caldwell & Cornwell 1975; Haftorn 1978; Yom-Tov & Mendelssohn 1978; Yom-Tov & Hilborn 1981; Davis et al. 1984; Drent et al. 1985; Morton & Pereyra 1985; Løfaldli 1985; Haftorn 1988). This may reflect either different degrees of energetic constraint (Martin 1987) or different strategies for parental investment. Parents that increase incubation effort as temperatures decrease may potentially be working at damagingly high metabolic rates (Drent & Daan 1980) or sacrificing their own body reserves to preserve their eggs' thermal environment (Haftorn 1988; Bryant 1988; Moreno 1989b). Alternatively, they may be working below their metabolic ceilings and have relatively unconstrained energy budgets during their incubation periods so that they can increase attendance without incurring fitness costs.

A comparative analysis of the life histories and ecological conditions of species falling into the two patterns of attendance with temperature might reveal which explanation was more general. If species that decreased attendance with improving conditions generally had biparental care or mate provisioning, a favourable nest microclimate, large body reserves, relatively small clutch masses or abundant food then relatively low energetic constraint may explain the relationship. However if, within a species, individuals with lower residual reproductive value, such as older birds, showed a greater relative increase in attendance with deteriorating conditions then we would suspect that differences in life history underlie the different patterns of attendance with temperature. Of course, this dichotomy in the pattern of variation in attendance with temperature oversimplifies real patterns and, in dotterel, there was some indication that attendance was reduced in very good weather conditions in contrast to their more general pattern of a declining attendance with deteriorating conditions. Similarly, birds may respond to poor weather or experimentally cooled eggs by increasing attendance but may eventually have to decrease attendance to allow self-maintenance (Davis et al. 1984) and nest attendance in the northern wheatear *Oenanthe oenanthe* may only have been energetically constrained in cold years (Haftorn 1988; Moreno 1989a). In very poor conditions, passerines may switch from rarely allowing their eggs to drop below the PZT to temporarily deserting their eggs (Morton & Pereyra 1985; Haftorn 1988). In contrast, dotterel appeared to gradually compromise their embryos' thermal environment with worsening



conditions (Fig. 7b), finally neglecting their eggs for long periods in very poor conditions (Chapter 4).

## MODELS OF INCUBATION SCHEDULING

There are several existing models of why or how birds schedule incubation (Davis et al. 1984; Haftorn 1988). Hainsworth et al. (1998) suggest that incubation bout duration will be determined by how a lone parent allocates time between self-maintenance and maintaining the thermal environment of the embryos stating that, for parents to increase investment in themselves, they should reduce the duration of steady-state incubation per incubation bout. Their model only considers the effect of incubation bout duration on parents' allocation of time between themselves and their eggs. During incubation, a bird's energy budget is generally a better currency for measuring its condition and ultimately its fitness than its allocation of time to feeding off the nest, which does not consider the consequent variation in the energetic costs of incubation. Egg rewarming can require more power than steady-state incubation (Haftorn & Reinertsen 1990; Andreev 1999) so that reducing incubation shift length and so increasing the proportion of shifts spent rewarming may push up energetic costs even though attendance is reduced. Hainsworth et al.'s (1998) predicted decrease in shift length to increase allocation of time towards self-maintenance may, in some ecological conditions, increase their energetic costs, at least partially cancelling out energetic gains made during the longer feeding trips.

The model for dotterel suggests that for a parent to improve its energy budget, it is more efficient to increase both its incubation shift and feeding trip durations, as eggs cool according to a negative exponential function so that fewer, longer trips result in less egg rewarming. The best incubation schedule to balance time spent feeding, energetic expenditure on incubation and the embryos' thermal environment will depend on the relative importance of steady-state incubation costs and egg rewarming costs. If, for example, unattended eggs were covered with plenty of good insulants, such as down, they might lose little more heat than when

incubated (Caldwell & Cornwell 1975), so that the energetic cost of incubation would be less dependent upon incubation shift length.

One model of incubation scheduling predicts that parents should end their incubation bout when their body reserves fall below a certain level (references in Davis et al. 1984; Chaurand & Weimerskirch 1994; Weimerskirch 1995). From this model there are two testable predictions based on variation in the level of body reserves. On average, dotterel lose mass through the incubation period so that we would predict that shift length should decrease correspondingly, as individuals will sooner hit the critical level of body reserves at which they leave the nest: shift length did decrease through the incubation period. We would also predict that individuals with greater body reserves should have longer incubation shifts between trips but there was no evidence for this (mass corrected for first egg date and body size was not significantly correlated with median of daily median shift lengths,  $r_s = -0.363$ ,  $P = 0.203$ ,  $N = 14$ , days selected as in previous test).

Another suggested model of incubation scheduling is that parents should warm their eggs up to a 'release' or temperature or 'set point' and then leave for a foraging trip (White & Kinney 1974; Zerba & Morton 1983; references in Davis et al. 1984; Turner 1994b). However, if the 'release' temperature was the optimal temperature for egg development or below, eggs may spend little or no time at this optimum, and 'release' temperatures little higher than the optimum could kill embryos (Williams 1996). In cold environments, where unattended eggs would rapidly cool below the 'release' temperature, this model would appear to allow embryos to spend little time at temperatures suitable for development. Alternatively, birds could have a short cycle of sitting bouts, which would allow them to follow of 'set point' model of incubation without sacrificing their embryos' thermal environment. For uniparental dotterel to use a 'release' temperature of 40°C (the upper end of the range of optimal developmental temperatures, Haftorn 1988, which gives incubation parameters closest to those observed) and achieve the same estimated amount of time below 20°C, under typical egg cooling conditions they would have 38 18.0 min feeding trips and 20.0 min incubation shifts per day, which would carry the high mean cost of 1.7W, and possibly increase the risk of predators

finding their nest through their more frequent movements. This model did not seem to fit uniparental dotterel's incubation scheduling, as median trip length was  $9.4 \pm 0.9$  min and median incubation bout duration was  $40.5 \pm 4.5$  min, with  $16.3 \pm 1.7$  trips per day. Moreover, coal tits *Parus ater*, Belding's Savannah Sparrow *Passerculus sandwichensis beldingi* and pied flycatchers *Ficedula hypoleuca* did not terminate their incubation bouts when their eggs reached a set point (Davis et al. 1984; Haftom & Reinertsen 1990).

Kendeigh's (1952) maximal food intake model of incubation scheduling reviewed in Drent et al. (1985) suggests that a House Wren *Troglodytes aedon* ended their foraging trips when their stomachs were full and the incubation bout finished when the contents were digested, with some influence of temperature. Drent et al. (1985) found that biparental common starlings' *Sturnus vulgaris* incubation scheduling was reasonably well described by Kendeigh's model. However, incubation did not appear to be very energetically expensive in common starlings and biparental care allowed the parents to spend more time foraging while achieving high nest attendance, so that their embryos probably spent little time at temperatures unsuitable for development: the influences on biparental common starlings' incubation schedule are probably quite different from those on a uniparental common starling (Reid et al. 2000) or on a uniparental dotterel nesting in a cold climate where the costs of incubation will be higher. We cannot test how well Kendeigh's model fits dotterel since we do not know how long it takes to fill up the stomach or digest its contents, but dotterels' incubation scheduling appears to trade off food intake, energy expenditure on incubation and the embryos' thermal environment so the maximal food intake model may be too simple.

Perhaps it is not surprising that none of the models of incubation scheduling appeared to adequately describe uniparental dotterel's incubation scheduling, as incubation scheduling varied between parental care systems, with time of day, the stage of incubation, past and current weather conditions and, possibly, the level of body reserves and the risk of nest predation. Elements of the different models might supply some of the constraints (such as digestive bottlenecks or buffering body reserves) or optimisation goals (such as balancing the

allocation of time between incubation and foraging) that together shape dotterel's pattern of incubation.

We constructed a model of incubating scheduling (Fig. 7a) that was one solution to balancing the energetic costs of incubation and the embryos' thermal environment. This model described how the energetic cost of incubation would vary with environmental conditions if dotterel adopted the least energetically expensive trip duration that never allowed their eggs to drop below a temperature suitable for development (the physiological zero temperature or PZT). This model provided a poor fit for dotterel's incubation scheduling, even in favourable conditions when dotterel should have been least energetically constrained from adopting this solution. In the most favourable conditions dotterel made shorter, more frequent trips than this model predicted, possibly because dotterel were striving for a better embryonic thermal environment than just maintaining the eggs above the index of PZT (as the rate of embryonic development increases with temperature between the PZT and the optimum, Spiers & Baummer 1990; Mathiu et al. 1994).

#### PROXIMATE CONTROLS ON NEST ATTENDANCE

Models of incubation often assume that birds control their eggs' temperature through their incubation scheduling. How do birds match their nest attendance to the temperature of their eggs? Birds may either return to the nest when they predict that their eggs will have cooled to a certain temperature or they may empirically measure the eggs' temperature with their brood patch (White & Kinney 1974; Davis et al. 1984). Experiments with heated and cooled eggs suggest that egg temperature may moderate incubation scheduling but does not entirely control it (Davis et al. 1984; Drent et al. 1985). Dotterel generally settled onto the nest for an incubation shift on return from a feeding trip, suggesting that they were generally predicting egg temperature (Davis et al. 1984; Bryan & Bryant 1999) although, in the absence of any apparent disturbance, they did occasionally leave the nest for another feeding trip immediately after settling on the eggs (pers. obs.), which might suggest occasional fine tuning of trip length to actual egg temperature.

## SAVING ENERGY BY SCHEDULING TRIPS IN BETTER ENVIRONMENTAL CONDITIONS

In uniparental dotterel, egg rewarming (including replacement of heat lost from the eggs during rewarming) accounted for  $39\% \pm 2\%$  of the total costs of uniparental incubation (estimated from the means of 38 nests). For any given level of nest attendance and trip length, dotterel were able to reduce their costs of egg re-warming by scheduling their trips away from the nest to coincide with periods of better weather when unattended eggs would cool more slowly. On a daily basis, uniparental dotterel scheduled their trips so that potential egg cooling rates were  $4\% \pm 1\%$  lower during trips than while they chose to sit. If dotterel were able to schedule all their daily time off the nest to coincide with the lowest egg cooling rates, cooling rates could be  $28\% \pm 1\%$  lower during trips. It is not surprising that their actual improvement falls well short of this: not only does it demand perfect prediction of the day's weather but also that there are no constraints such as maintenance of the egg's thermal environment, depletion of body reserves or digestive bottlenecks during feeding trips (Kersten & Visser 1996) and also no unplanned trips due to predators or other disturbances.

Dotterel may have reduced their unattended eggs' cooling rates by scheduling their trips in response to current weather conditions or making predictions of future weather, or they may have used the simple rule of scheduling trips according to the typical daily variation in cooling rates (Cartar & Montgomerie 1985). Scheduling trips to coincide with low cooling rates reduces eggs' exposure to temperatures unsuitable for development as well as reducing rewarming costs. Biparental dotterel did not schedule their trips to coincide with low egg cooling rates. This suggests that it is the increased energetic costs of higher egg cooling rates, which two parents can bear more easily than a single parent, rather than more time below the PZT (which should be similarly important to uniparental and biparental dotterel) that uniparental dotterel are minimising through their scheduling. During darkness, trips were not scheduled to reduce egg cooling rates but uniparental and biparental nests showed similar pattern of hourly attendance, with midnight and pre-dawn peaks in feeding activity. This suggests that there are other factors influencing trip scheduling such as prey availability, predator activity or depletion of body reserves over time, and such factors may also operate during daytime (Baerends et al. 1970).

## CONSTRAINTS ON INCUBATION SCHEDULING

There appeared to be constraints on incubation scheduling other than balancing incubation scheduling and energy budgets. On a site heavily used by ravens, a greater proportion of trips to and from the nest were made between sunset and sunrise than on a site where avian predators were less abundant and where mammalian predators were more active: this may have reduced the probability of visually hunting avian predators detecting the nest (Hohman 1986). However, only very tentative conclusions can be drawn from a comparison of only two sites, between which many influential factors other than the predator assemblage may vary. Incubation scheduling did not appear to be constrained by the changing thermal sensitivity of the embryos. Although avian embryos are generally thought to become more sensitive to chilling closer to hatch, dotterel's eggs spent more time at low temperatures as incubation progressed. Dotterel probably do not experience this potential constraint on scheduling as their embryos can survive several hours of chilling to very low temperatures throughout the incubation period (Chapter 4).

## ENERGETIC CONSTRAINT AND PARENTAL CARE SYSTEMS

High costs of incubation and any consequent energetic constraint have implications for parental care systems and hence breeding systems. Seeking a new mate often means deserting the current one: for polygamy to be a successful strategy, the individual must gain more reproductive success through making new breeding attempts than it loses through leaving its deserted mate to care alone (Owens & Bennett 1997; Székely & Cuthill 2000). Successful uniparental incubation is a prerequisite for the evolution of mate desertion and, once uniparental care is established, there may be increased selective pressure for the deserted mate to reduce and successfully manage the high energetic costs of incubation. In dotterel's cool environment the energetic costs of incubation are potentially high and uniparental dotterel exhibited behavioural mechanisms to reduce the energetic cost of incubation and limit their expenditure according to the degree of energetic constraint they experienced. However, dotterel sometimes deserted clutches, especially during prolonged poor weather or snow lie and late in the season (D.P. Whitfield unpublished data). These

desertions may represent periods when single parents could not successfully manage the energetic costs of incubation (Haftorn 1988) and this is supported by the apparently lower desertion rate of late-season biparental nests compared with uniparental nests (D.P. Whitfield unpublished data).

#### **BALANCING INVESTMENT IN THE YOUNG AND INVESTMENT IN SELF-MAINTENANCE**

Life-history theory predicts that animals should balance their investment in their current breeding attempt against any consequent reductions in their future survival and productivity, so that their current investment may depend upon the current environmental conditions (Erikstad et al. 1998). Dotterel's allocation of time and energy between themselves and their eggs appeared to depend upon the degree of energetic constraint they were experiencing as they varied investment in incubation according to their overall energetic costs and, probably, according to their level of body reserves. Dotterel capped their investment in their current breeding attempt, presumably to increase their probability of surviving to another breeding attempt. A reduction in investment in incubation can reduce the probability of success of a breeding attempt by increasing the incubation period (Chapter 4), the risk of clutch predation (Drent 1970) or the risk of thermal damage to the embryos (Webb 1987).

However, a male dotterel that lost its clutch by capping investment is likely to have further breeding opportunities: dotterel can make at least two replacement breeding attempts within the same season (D.P. Whitfield unpublished data) and adult shorebird survival between seasons is relatively high (Evans & Pienkowski 1984). Dotterel's strategy for investment in the current breeding attempt may then maximize lifetime reproductive success by trading off the success of the current breeding attempt against their own survival and ability to produce future offspring.

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## References

- Aldrich, T.W. & Raveling, D.G. 1983. Effects of experience and body weight on incubation behaviour of Canada geese. Auk , 100, 670-679.
- Andreev, A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich , 70, 13-22.
- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk , 95, 459-471.
- Baerends, G.P., Drent, R.H., Glas, P. & Groenewold, H. 1970. An ethological analysis of incubation behaviour in the Herring Gull. Behaviour Supplement , 17, 135-234.
- Bakken, G.S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk , 107, 587-594.
- Bang, P. & Dahlstrøm, P. 1990. Animal tracks and signs. 2nd edn. London: Collins.
- Batt, B.D. & Cornwell, G.W. 1972. The effects of cold on Mallard embryos. Journal of Wildlife Management , 36, 745-751.
- Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating Starlings (*Sturnus vulgaris*). Physiological Zoology , 57, 26-31.
- Biebach, H. 1986. Energetics of rewarming a clutch in Starlings (*Sturnus vulgaris*). Physiological Zoology , 59, 69-75.
- Bruinzeel, L.W. & Piersma, T. 1998. Cost reduction in the cold: heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. Ibis , 140, 323-328.
- Bryan, S.M. & Bryant, D.M. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in Great Tits, *Parus major*. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 266, 157-162.
- Bryant, D.M. 1988. Energy expenditure and body mass changes as measures of reproductive cost in birds. Functional Ecology , 2, 23-34.



- Bryant, D.M. & Tatner, P. 1991. Intraspecific variation in avian energy expenditure: correlates and constraints. Ibis , 133, 236-245.
- Calder, W.A. & King, J.R. 1974. Thermal and caloric relations of birds. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 259-413. New York: Academic Press.
- Caldwell, P.J. & Cornwell, G.W. 1975. Incubation behaviour and temperatures of the Mallard duck. Auk , 92, 706-731.
- Campbell, R.C. 1989. Statistics for biologists . Third Edition edn. Cambridge: Cambridge University Press.
- Carey, C. 1980. The ecology of avian incubation. BioScience , 30, 819-824.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour , 95, 261-289.
- Cartar, R.V. & Montgomerie, R.D. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. The Condor , 89, 252-260.
- Chaurand, T. & Weimerskirch, H. 1994. Incubation routine, body-mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. Ibis , 136, 285-290.
- Coleman, R.M. & Whittall, R.D. 1988. Clutch size and the cost of incubation in the Bengalese Finch (*Lonchura striata* var. *domestica*). Behavioural Ecology and Sociobiology , 23, 367-372.
- Cooper, S.J. & Swanson, D.L. 1994a. Seasonal acclimatization of thermoregulation in the Black-capped Chickadee. The Condor , 96, 638-646.
- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Croxall, J.P. 1982. Energy cost of incubation and moult in petrels and penguins. Journal of Animal Ecology , 51, 177-194.
- Davis, S.D., Williams, J.B., Adams, W.J. & Brown, S.L. 1984. The effect of egg temperature on attentiveness in the Belding's Savannah Sparrow. Auk , 101, 556-566.

- Dawson,W.R., Marsh,R.L., Buttemer,W.A. & Carey,C. 1983b. Seasonal and geographic variation of cold resistance in house finches *Carpodacus mexicanus*. Physiological Zoology , 56,
- Deeming,D.C. & Ferguson,M.W.J. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Egg incubation: its effects on embryonic development in birds and reptiles (Ed. by D.C.Deeming & M.W.J.Ferguson), pp. 147-171. Cambridge: Cambridge University Press.
- Drent,R.H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Supplement , 17, 1-132.
- Drent,R.H. 1975. Incubation. In: Avian Biology (Ed. by D.S.Farner & J.R.King), pp. 333-420. New York: Academic Press.
- Drent,R.H. & Daan,S. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea , 68, 225-252.
- Drent,R.H., Postuma,K.H. & Joustra,T. 1970. The effect of egg temperature on incubation behaviour in the Herring Gull. Behaviour Supplement , 17, 235-260.
- Drent,R.H., Tinbergen,J.M. & Biebach,H. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands Journal of Zoology, 35, 103-123.
- Dutenhoffer,M.S. & Swanson,D.L. 1996c. Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. Physiological Zoology , 69, 1232-1254.
- Eichholz,M.W. & Sedinger,J.S. 1999. Regulation of incubation behavior in Black Brant. Canadian Journal of Zoology , 77, 249-257.
- Erikstad,K.E. 1986. Relationship between weather, body condition and incubation rhythm in Willow Grouse. Fauna norvegica Ser. C Cinclus , 9, 7-12.
- Erikstad,K.E., Fauchald,P., Tveraa,T. & Steen,H. 1998. On the cost of reproduction in long-lived birds: The influence of environmental variability. Ecology , 79, 1781-1788.
- Erikstad,K.E., Myrberget,S. & Blom,R. 1982. Territorial crows as predators on Willow Ptarmigan nests. Journal of Wildlife Management , 46, 109-114.

- Evans,P.R. & Pienkowski,M.W. 1984. Population dynamics of shorebirds. In: Shorebirds, breeding behaviour and populations (Ed. by J.Burger & B.L.Olla), pp. 83-123. New York: Plenum Press.
- Fernández,G.J. & Reboresda,J.C. 2000. Egg losses and nest desertion in Greater Rheas. Ibis , 142, 29-34.
- Galbraith,H., Murray,S., Duncan,K., Smith,R., Whitfield,D.P. & Thompson,D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. Ibis , 135, 148-155.
- Green,R.E., Hirons,G.J.M. & Cresswell,B.H. 1990. Foraging habitats of female Common Snipe *Gallinago gallinago* during the incubation period. Journal of Applied Ecology , 27, 325-335.
- Haftorn,S. 1978. Energetics of incubation by the Goldcrest *Regulus regulus* in relation to ambient air temperatures and geographical distribution of the species. Ornis Scandinavica , 9, 22-30.
- Haftorn,S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Ornis Scandinavica , 19, 97-110.
- Haftorn,S. & Reinertsen,R.E. 1982. Regulation of body temperature and heat transfer to eggs during incubation. Ornis Scandinavica , 13, 1-10.
- Haftorn,S. & Reinertsen,R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit. Auk , 102, 470-478.
- Haftorn,S. & Reinertsen,R.E. 1990. Thermoregulatory and behavioral responses during incubation of free-living Pied Flycatchers *Ficedula hypoleuca*. Ornis Scandinavica , 21, 255-264.
- Hainsworth,F.R., Moonan,T., Voss,M.A., Sullivan,K.A. & Weathers,W.W. 1998. Time and heat allocations to balance conflicting demands during intermittent incubation by Yellow-eyed Juncos. Journal of Avian Biology , 29, 113-120.
- Harris,H.J. 1970. Evidence of stress response in breeding Blue-winged Teal. Journal of Wildlife Management , 34, 747-755.
- Hart,J.S. 1962d. Seasonal acclimatization in four species of small wild birds. Physiological Zoology , 35, 224-236.

- Harvey, J.M. 1971. Factors affecting Blue Goose nesting success. Canadian Journal of Zoology , 49, 223-234.
- Harvey, W.F., Hepp, G.R. & Kennamer, R.A. 1989. Body mass dynamics of Wood Ducks during incubation: individual variation. Canadian Journal of Zoology , 67, 570-574.
- Hegyí, Z. & Sasvári, L. 1998. Parental condition and breeding effort in waders. Journal of Animal Ecology , 67, 41-53.
- Hepp, G.R., Kennamer, R.A. & Harvey, W.F. 1990. Incubation as a reproductive cost in Wood Ducks. Auk , 107, 756-764.
- HMSO 1982. Observer's Handbook. 4th edn. London: HMSO.
- Hohman, W.L. 1986. Incubation rhythms of Ring-necked Ducks. The Condor , 88, 290-296.
- Hollom, P.A.D. 1980. The Popular Handbook of British Birds. 4th edn. London: H. F. & G. Witherby Ltd.
- Holt, S., Whitfield, D.P., Duncan, K., Rae, S. & Smith, R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? Journal of Avian Biology , 33, 219-224
- Horsfield, D. & Thompson, D.B. 1996. The uplands: guidance on terminology regarding altitudinal zonation and related terms. Information and Advisory Note 26. Battleby, UK: SNH
- Inglis, I.R. 1977. The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. Animal Behaviour , 25, 747-764.
- Jones, G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. Journal of Animal Ecology , 56, 229-245.
- Kálás, J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Kálás, J.A. & Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). Auk , 101, 838-847.
- Kálás, J.A. & Løfaldli, L. 1987. Clutch size in the Dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? Ornis Scandinavica , 18, 316-319.
- Kersten, M. & Piersma, T. 1986. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea , 75, 175-188.

- Kersten, M. & Visser, W. 1996. The rate of food processing in the Oystercatcher: Food intake and energy expenditure constrained by a digestive bottleneck. Functional Ecology , 10, 440-448.
- Khaskin, V.V. 1961. Heat exchange in birds' eggs on incubation. Biophysics , 6, 91-99.
- Konratiev, A.J. 1982. Biology of waders in the tundras of the north-east of Asia. Academy of Sciences of the USSR: Nauka, Moscow
- Korschgen, C.E. 1977. Breeding stress of female eiders in Maine. Journal of Wildlife Management , 41, 360-373.
- Koteja, P. 1986e. Maximum cold induced oxygen consumption in the House Sparrow *Passer domesticus* L. Physiological Zoology , 59, 43-48.
- Lessells, C.M. 1986. Brood size in Canada Geese: a manipulation experiment. Journal of Animal Ecology , 55, 669-690.
- Liknes, E.T. & Swanson, D.L. 1996f. Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in White-breasted Nuthatches *Sitta carolinensis* and Downy Woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. Journal of Avian Biology , 27, 279-288.
- Løfaldli, L. 1985. Incubation rhythms in the Great Snipe *Gallinago media*. Holarctic Ecology , 8, 107-112.
- MacLean, S.F.Jr. & Pitelka, F.A. 1971. Seasonal patterns of abundance in tundra arthropods near Barrow, Alaska. Arctic , 24, 19-40.
- MacMullan, R.A. & Eberhardt, L.L. 1953. Tolerance of incubating pheasant eggs to exposure. Journal of Wildlife Management , 17, 322-330.
- Mallory, M.L. & Weatherhead, P.J. 1993. Incubation rhythms and mass loss of Common Goldeneyes. The Condor , 95, 849-859.
- Martin, T.E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics , 18, 453-487.
- Martin, T.E. & Ghalambor, C.K. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? American Naturalist , 153, 131-139.
- Mathiu, P.M., Dawson, W.R. & Whittow, G.C. 1994. Thermal responses of late embryos and hatchlings of the Sooty Tern. The Condor , 96, 280-294.

- Mertens, J.A.L. 1977. The energy requirements for incubation in Great Tits, *Parus major* L. Ardea , 65, 184-196.
- Monaghan, P. & Nager, R.G. 1997. Why don't birds lay more eggs? Trends In Ecology & Evolution , 12, 270-274.
- Moreno, J. 1989a. Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe*. Ardea , 77, 107-115.
- Moreno, J. 1989b. Strategies of mass change in breeding birds. Biological Journal of the Linnean Society , 37, 297-310.
- Moreno, J., Gustafsson, L., Carson, A. & Pärt, T. 1991. The cost of incubation in relation to clutch-size in the Collared Flycatcher *Ficedula albicollis*. Ibis , 133, 186-193.
- Moreno, J. & Sanz, J.J. 1994. The relationship between the energy-expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. Journal of Avian Biology , 25, 125-130.
- Morton, M.L. & Pereyra, M.E. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). Auk , 102, 25-37.
- Nethersole-Thompson, D. 1973. The Dotterel. Glasgow: Collins.
- Norton, D.W. 1972. Incubation schedules of four species of Calidrine sandpipers at Barrow, Alaska. The Condor , 74, 164-176.
- Norton, D.W. 1973. Ecological energetics of Calidrine sandpipers breeding in northern Alaska. PhD thesis, University of Alaska, Fairbanks.
- Norusis, M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Gorinchem: SPSS Ltd.
- Owens, I.P.F. & Bennett, P.M. 1997. Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 264, 1103-1110.
- Paganelli, C.V., Olszowka, A. & Ar, A. 1974. The avian egg: surface area, volume and density. The Condor , 76, 319-325.
- Paladino, F.V. 1989. Constraints of bioenergetics on avian population dynamics. Physiological Zoology , 62, 410-428.
- Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.

- Pulliainen,E. & Saari,L. 1992. Body mass and physical condition of breeding Dotterels *Charadrius morinellus* in Finland. Oecologia Montana , 1, 1-4.
- Reed,A., Hughes,R.J. & Gauthier,G. 1995. Incubation behaviour and body mass in Greater Snow Geese. The Condor , 97, 993-1001.
- Reid,J.M., Monaghan,P. & Ruxton,G.D. 1999. The effect of cooling rate on starling, *Sturnus vulgaris*, incubation strategy. Animal Behaviour , 58, 1161-1167.
- Reid,J.M., Monaghan,P. & Ruxton,G.D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 267, 37-41.
- Ricklefs,R.E. 1969. An analysis of nesting mortality in birds. Smiths. Cont. Zool. 9, 1-48.
- Ricklefs,R.E. 1974. Energetics of reproduction in birds. In: Avian energetics (Ed. by R.A.J.Paynter), pp. 152-297. Nuttall Ornithological Club.
- Root,T.L., O'Connor,T.P. & Dawson,W.R. 1991g. Standard metabolic level and insulative characteristics of Eastern House Finches, *Carpodacus mexicanus* (Müller). Physiological Zoology , 64, 1279-1295.
- Rosenmann,M. & Morrison,P. 1974h. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O<sub>2</sub>. American Journal of Physiology , 226, 490-495.
- Sanz,J.J. 1995. Environmental restrictions on reproduction in the Pied Flycatcher *Ficedula hypoleuca*. Ardea , 83, 421-430.
- Sibly,R. & McCleery,R. 1985. Optimal decision rules for herring gulls. Animal Behaviour , 33, 449-465.
- Siikamaki,P. 1995. Are large clutches costly to incubate? - the case of the Pied Flycatcher. Journal of Avian Biology , 26, 76-80.
- Spiers,D.E. & Baummer,S.C. 1990. Embryonic development of Japanese Quail (*Coturnix coturnix japonica*) as influenced by periodic cold exposure. Physiological Zoology , 63, 516-535.
- Swanson,D.L. 1990i. Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the Dark-eyed Junco (*Junco hyemalis*). Auk , 107, 561-566.

- Székely, T. & Cuthill, I.C. 2000. Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 267, 2087-2092.
- Thomson, D.L., Furness, R.W. & Monaghan, P. 1998a. Field metabolic rates of Kittiwakes *Rissa tridactyla* during incubation and chick rearing. Ardea , 86, 169-175.
- Thomson, D.L., Monaghan, P. & Furness, R.W. 1998b. The demands of incubation and avian clutch size. Biological Review , 73, 293-304.
- Tombre, I.M. & Erikstad, K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Tøien, Ø. 1989. Effect of clutch size on efficiency of heat transfer to cold eggs in bantam hens. In: Physiology of cold adaptation in birds (Ed. by C. Bech & R.E. Reinertsen), pp. 305-313. New York: Plenum Press.
- Tulp, H., Schekkerman, H., Piersma, T., Jukema, J., de Goeij, P., & van de Kam, J. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. 61. Zeist, The Netherlands: WIWO
- Turner, J.S. 1991. The thermal energetics of incubated bird eggs. In: Egg incubation: Its effects on embryonic development in birds and reptiles (Ed. by D.C. Deeming & M.W.J. Ferguson), pp. 117-146. Cambridge: Cambridge University Press.
- Turner, J.S. 1994a. Thermal impedance of a contact-incubated birds egg. Journal of Thermal Biology , 19, 237-243.
- Turner, J.S. 1994b. Time and energy in the intermittent incubation of birds' eggs. Israel Journal of Zoology , 40, 519-540.
- Turner, J.S. 1994c. Transient-state thermal-properties of contact-incubated chicken eggs. Physiological Zoology , 67, 1426-1447.
- Turner, J.S. 1997. On the thermal capacity of a bird's egg warmed by a brood patch. Physiological Zoology , 70, 470-480.
- Vleck, C.M. 1981a. Energetic cost of incubation in the Zebra Finch. The Condor , 83, 229-237.
- Vleck, C.M. 1981b. Hummingbird incubation: female attentiveness and egg temperature. Oecologia , 51, 199-205.



- Vleck, C.M. & Kenagy, G.J. 1980. Embryonic metabolism of the Fork-tailed Storm Petrel: physiological patterns during prolonged and interrupted incubation. Physiological Zoology , 53, 32-42.
- Walsberg, G.E. 1983. Avian ecological energetics. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 161-220. New York: Academic Press.
- Ward, D. 1990. Incubation temperatures and behaviour of Crowned, Black-winged, and Lesser Black-winged Plovers. Auk , 107, 10-17.
- Webb, D.R. 1987. Thermal tolerance of avian embryos: A review. The Condor , 89, 874-898.
- Webb, D.R. & King, J.R. 1983. An analysis of the heat budgets of the eggs and nest of the White-crowned Sparrow, *Zonotrichia leucophrys*, in relation to parental attentiveness. Physiological Zoology , 56, 493-505.
- Weimerskirch, H. 1995. Regulation of foraging trips and incubation routine in male and female Wandering Albatrosses. Oecologia , 102, 37-43.
- Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecology and Evolution , 11, 384-388.
- White, F.N. & Kinney, J.L. 1974. Avian incubation. Science , 186, 107-115.
- Wiebe, K.L. & Martin, K. 1997. Effects of predation, body condition and temperature on incubation rhythms of White-tailed Ptarmigan. Wildlife Biology , 3, 219-227.
- Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Williams, J.B. 1996. Energetics of avian incubation. In: Avian energetics and nutritional ecology (Ed. by C. Carey), pp. 375-415. New York: Chapman & Hall.
- Williams, J.B. & Dwinell, B. 1990. Incubation energetics of female Savannah Sparrows. Physiological Zoology , 63, 353-372.
- Wilson, H.R. 1991. Physiological requirements of the developing embryo: temperature and turning. In: Avian Incubation (Ed. by S.G. Tullet), pp. 145-156. Rushenden, U.K.: Butterworth-Heinemann Ltd.
- Yom-Tov, Y. & Hilborn, R. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia , 48, 234-243.

Yom-Tov, Y. & Mendelssohn, H. 1978. Incubation behaviour of the Dead Sea sparrow. The Condor, 80, 340-343.

Zerba, E. & Morton, M.L. 1983. Dynamics of incubation in Mountain White-crowned Sparrows. The Condor, 85, 1-11.

## Chapter 4

### CONSEQUENCES OF REDUCED NEST ATTENDANCE IN THE EURASIAN DOTTEREL

Sue Holt, D. Philip Whitfield & David M. Bryant

#### ABSTRACT

Eurasian dotterel (*Charadrius morinellus*) have variable parental care during incubation: the majority of breeding attempts are cared for by the male alone but a proportion of late-season nests are incubated by both parents. Uniparental dotterel must resolve the conflicting requirements of maximising nest attendance while spending sufficient time feeding to cover their energy requirements in a demanding Alpine environment. Uniparental nests were attended less and neglected more frequently than biparental nests. During periods of neglect, dotterel embryos, even up to the point of hatch, survived numerous long periods of chilling to low temperatures. Dotterel embryos' tolerance of chilling permits successful uniparental incubation in an environment where energetic demands can compel long trips from the nest. However, low nest attendance means that embryos spend more time below a temperature at which development normally occurs; accordingly, the length of the incubation period increased with decreasing nest attendance. At biparental nests, dotterel can have high nest attendance and, by extrapolation, shorter incubation periods, which are probably more successful. In poor conditions, energetically stressed uniparental incubators can neglect the eggs for long periods, but at the cost of an increased incubation period.

## INTRODUCTION

During the incubation period of birds the eggs are vulnerable to many dangers. The probability of egg-loss will be a function of the duration of the incubation period (Johnson 1979). For example, the longer the incubation period, the greater the probability of a predator finding the nest (Tombre & Erikstad 1996), or a large grazing mammal trampling it. A short incubation period should be favoured, therefore. Embryo development only takes place above the physiological zero temperature (PZT, Drent 1975) and incubation period increases with decreasing embryo temperature (Boersma & Wheelwright 1979; Vleck & Kenagy 1980; reviewed in Spiers & Baummer 1990). To minimise the incubation period a parent must constantly maintain the eggs at the optimal developmental temperature. Species with biparental incubation (e.g. Smith et al. 1995), those in which the incubating parent is fed by their mate (Morton & Pereyra 1985; Martin & Ghalambor 1999) and those in which the incubating parent uses stored fat reserves as fuel through the incubation period (Reed et al. 1995) may be able to achieve high nest attendance (the proportion of time the clutch is incubated, Norton 1972; reviewed in Drent et al. 1985), and embryo temperature may seldom drop below the PZT. However, in species where a lone parent must leave the nest at intervals to feed, the eggs may spend periods below the PZT (Miskelly 1989). These temporary pauses in development may extend the incubation period (Vleck & Kenagy 1980; Drent et al. 1985; Haftorn 1988; Spiers & Baummer 1990).

In a cold environment, as well as extending the incubation period, low nest attendance may expose the eggs to chilling. Relatively short periods of chilling may kill or have sub-lethal detrimental effects on embryos of most species (Batt & Cornwell 1972). Webb (1987) estimates embryonic chilling tolerance of 16°C for short periods of exposure or 36°C for several hours. There are exceptions to this (e.g. MacMullan & Eberhardt 1953; Lill 1979), most notably in birds such as the Procellariiformes where breeding system or feeding ecology compel long absences from the nest (e.g. Boersma 1982; Chaurand & Weimerskirch 1994). In species with uniparental intermittent incubation, there may be occasions, such as when food availability is low or when energetic costs of thermoregulation are high (Webb 1987),

when the parent is absent from the nest for long periods. The embryos of such species should be relatively tolerant of periods of exposure to low temperatures.

Eurasian dotterel *Charadrius morinellus* nest on open ground in the cool arctic-alpine zone, so unattended eggs will usually cool relatively rapidly below the PZT (Chapter 3). The cool climate will also cause relatively high energy demands for parental thermoregulation (Piersma & Morrison 1994). Most dotterel breeding attempts are cared for by the male alone but incubation is shared by both parents at a proportion of nests (Cramp & Simmons 1983; D.P. Whitfield unpublished). A uniparental male must maximise nest attendance and the time the embryos spend above the PZT, while spending sufficient time feeding off the nest to meet his own energy requirements (Kálás 1986). In this chapter we test whether nests cared for by the male alone were attended less than those cared for by both parents. We investigate whether uniparental nests were neglected more frequently than biparental nests and whether neglect occurred more frequently at uniparental nests in environmental conditions when they would have been more energetically constrained. We then investigate the consequences of reduced nest attendance: was there is a penalty for spending time off the nest in terms of an extended incubation period and did dotterel embryos survive chilling during neglect?

## METHODS

Incubation period durations were recorded between 1987-1994 and 1996-1998 on five low- and mid-alpine (Horsfield & Thompson 1996) sites in the Central Highlands of Scotland. Data on nest attendance were collected from two of these Low-Alpine sites, separated by 8km, in 1997 and 1998.

Data on nest attendance (the percentage of time nests were incubated, Norton 1972) were collected using a small flexible temperature probe fixed at the centre of the nest, logged at 35s intervals by a Tinytag datalogger (Gemini Data Loggers (UK) Ltd, Chichester, UK). The accuracy of nest attendance data obtained from nest temperature probes was confirmed from opportunistic visual records of attendance at logged nests (Chapter 3). In our measure of

overall nest attendance we only included absences from the nest of at least 140 seconds. It is likely that shorter trips would not be accurately detected from temperature traces at all nests under all weather conditions. Embryo temperature would be unlikely to fall below the PZT during this time (PZT lies between 20 and 27°C in chickens, Wilson 1991, though it is likely to vary between species, Webb 1987).

Nests were classified as biparental if a female was even seen incubating after clutch completion (although this will have misclassified a small percentage of biparental nest as uniparental when, by chance, the female was never seen sitting, Holt et al. 2002).

Dotterel's most frequent clutch size is three (Cramp & Simmons 1983). Incubation starts when the first egg is laid but nest attendance is initially low and increases as further eggs are laid (Kálás 1986). We use incubation period here to refer to the period from the date when the first egg was laid to the date when the last chick hatched (i.e. the period of risk of clutch failure; the more usual definition of incubation period from last egg laid to last egg hatched deducts 3 days for two 1.5d laying intervals, Nethersole-Thompson 1973; Cramp & Simmons 1983). First egg date was directly observed or estimated for incomplete clutches by subtracting 1.5 days per egg (Cramp & Simmons 1983). Females that do not assist with incubation desert the day that the clutch is completed (D.P. Whitfield unpublished) so, at two uniparental nests found with full clutches and where the female was still present, we estimated the first egg date by assuming that the female had just completed the clutch that day. Hatch date was observed or, in some cases, ascertained from the logged temperature traces. Most broods left the nest early in the morning and, based on other observations, we assumed that these completed hatch the day before departure from the nest.

Clutches were classed as trampled when eggs were found crushed into the nest and/or lying dented or broken outside the nest cup with their contents uneaten. Clutches were classed as depredated when they disappeared before the expected hatch date and/or when shell remains with beak or tooth marks or predator faeces, urine or feathers were found in or by the nest. Clutches were considered to have been deserted when no further attendance at the

nest was recorded (over a period of at least three days). Chicks were assumed to have fledged if they were known to survive to at least 18 days old (the fledging period is between 17 and 30+ days, D.P. Whitfield unpublished).

Air temperature (in a radiation shield 1.2 m above ground) and ground temperature (10cm below the ground surface) were logged at least every 3.5 minutes from a Tinytag or Logit (DCP Microdevelopments Ltd., Cambridge, UK) thermister.

The energetic cost of thermoregulation were estimated according to Wiersma & Piersma's (1994) model of variation in the costs of thermoregulation with weather variables (Chapter 3). The energetic cost of incubation was estimated from measurements from a simulated clutch, nest and brood patch exposed to different weather conditions (Chapter 3).

The availability of adults of the favoured prey *Tipula montana* (a crane fly) was determined from visual transects (Chapter 3).

We analysed data using SPSS (Norusis 1990) and give two-tailed probabilities. Means are quoted  $\pm$  95% C.L.

## RESULTS

Were uniparental nests attended less than biparental nests?

Biparental nests were attended for a significantly greater percentage of time than uniparental nests during the same time period, on the same site (Wilcoxon signed-ranks test:  $Z=2.201$ ,  $N=6$ ,  $P=0.028$ , biparental nests received a median of 13.1% more attendance than uniparental nests (range 5.4% to 21.2% more), a median of 15.7 days compared in pairs of nests, Fig. 1). The attendance at one male's nests was recorded as 96.5% in 1997 when biparental and 80.9% in 1998 when uniparental (23.7 and 14.1 days logged, respectively, neither nest in the previous sample, paired with the same female and on the same site in both years).

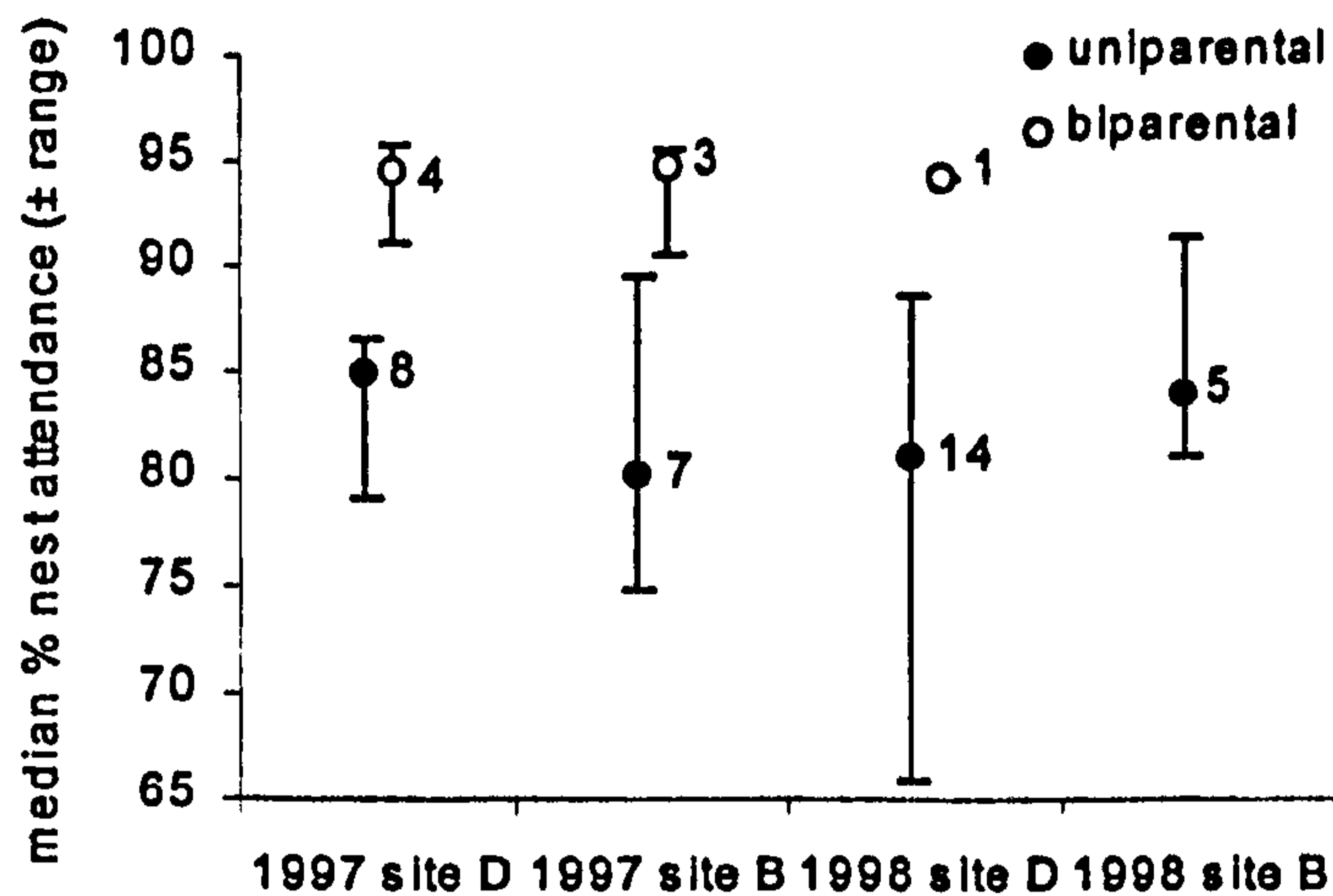


Figure 1. Median ( $\pm$  range) percentage nest attendance of 34 uniparental and eight biparental nests logged for at least five days. The sample size of nests is noted next to the median value.

Were uniparental nests neglected more frequently than biparental nests?

There was a non-significant tendency amongst nests in the above matched pair sample for biparental nests to have fewer absences of more than two hours per day than uniparental nests (Wilcoxon signed-ranks test:  $Z=1.826$ ,  $N=6$ ,  $P=0.068$ , a median of 0.19 more long trips per day for uniparental nests than for paired biparental nest). The power of this test was especially low due to ties, since no long trips were made for several nests. When uniparental and biparental nests, logged for at least five days were compared on an unmatched basis (Fig. 2) significantly more long trips were made from uniparental nests than from biparental nests (Mann-Whitney U-test:  $U=22.5$ ,  $N_1=15$ ,  $N_2=7$ ,  $P=0.026$ , median number of trips of more than two hours per day: biparental 0.00, uniparental 0.21). The sample for this test was confined to 1997 since there was only one biparental nest in 1998.



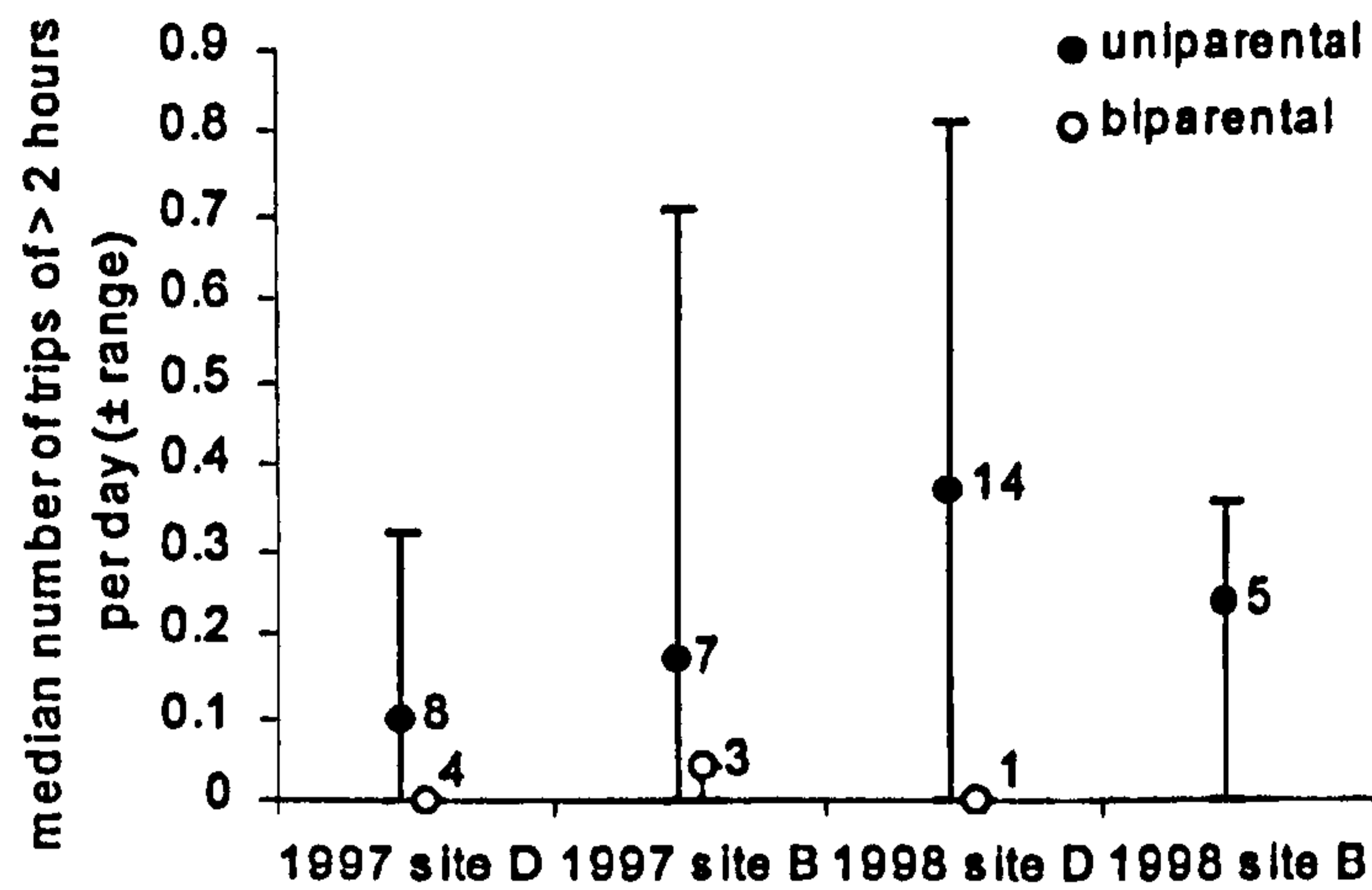


Figure 2. Median ( $\pm$  range) number of trips of more than two hours per day from 34 uni- and 8 biparental nests logged for at least five days. The sample size of nests is noted next to the median value.

Were uniparental nests neglected more frequently in more unfavourable energetic conditions? Within nests, egg neglect occurred on a significantly greater proportion of days in unfavourable energetic conditions than in favourable energetic conditions (Fig. 3, Wilcoxon signed ranks test comparing the daily incidence of neglect within uniparental nests:  $Z=3.578$ ,  $N=24$ ,  $P<0.001$ , egg neglect occurred on a  $0.407 \pm 0.143$  greater proportion of days in unfavourable conditions than favourable conditions, unfavourable days were when no *T. montana* adults were available and the estimated combined costs of steady state incubation and thermoregulation over both the current and previous five days were greater than the mean, favourable days were when either *T. montana* were available or the estimated combined costs of steady state incubation and thermoregulation over both the current and previous five days were less than the mean, following Chapter 3).

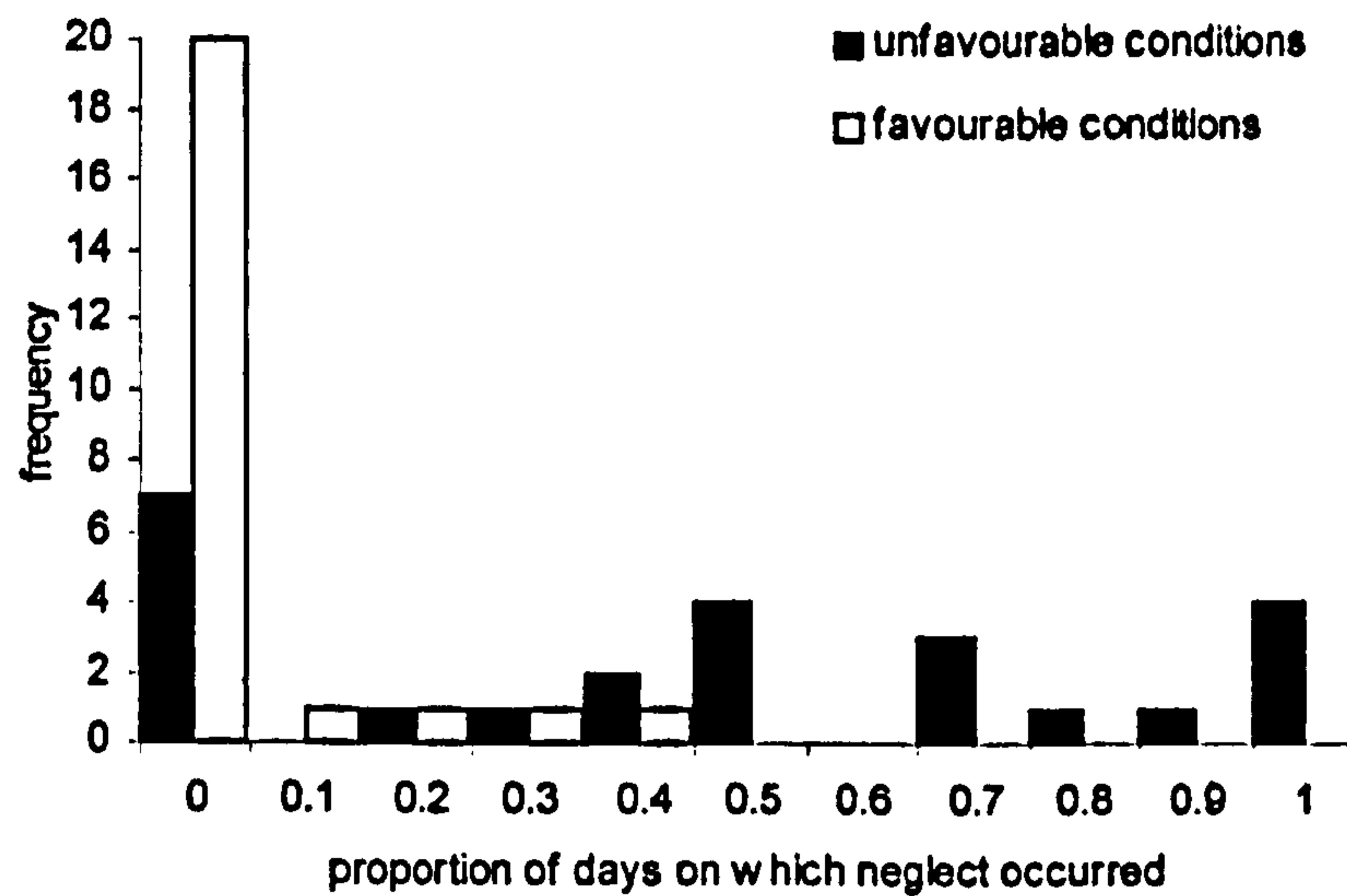


Figure 3. Egg neglect in favourable and unfavourable energetic conditions (favourable conditions were when the combined energetic costs of incubation and thermoregulation over both the current and the preceding five days were less than the mean value or when *Tipula montana* adults were available; unfavourable conditions were when the combined energetic costs of incubation and thermoregulation over both the current and the preceding five days were greater than the mean value and *Tipula montana* adults were unavailable). Each nest contributed a datum for favourable conditions and a datum for unfavourable conditions.

Did the duration of the incubation period vary with nest attendance?

The duration of the incubation period of dotterel was varied from 26 to 36 days ( $N=66$ , Fig. 4), with a median of 29 days. Incubation period duration was significantly negatively correlated with nest attendance (Spearman rank correlation:  $r_s=-0.86$ ,  $N=11$ ,  $P=0.001$ , the sample was confined to nests where at least 75% of the incubation period between clutch completion and hatch was logged, Fig. 5).

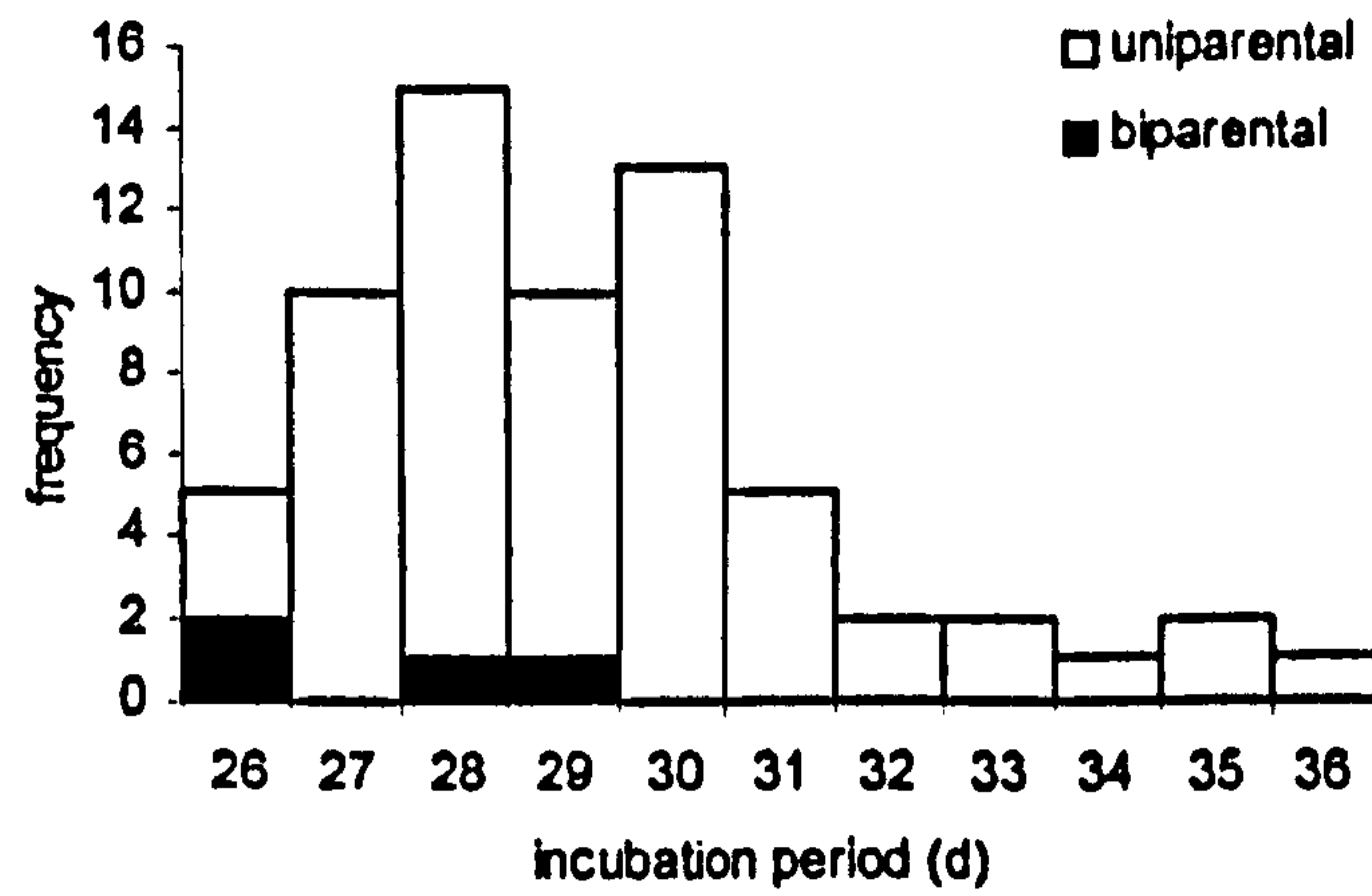


Figure 4. Incubation period durations in dotterel

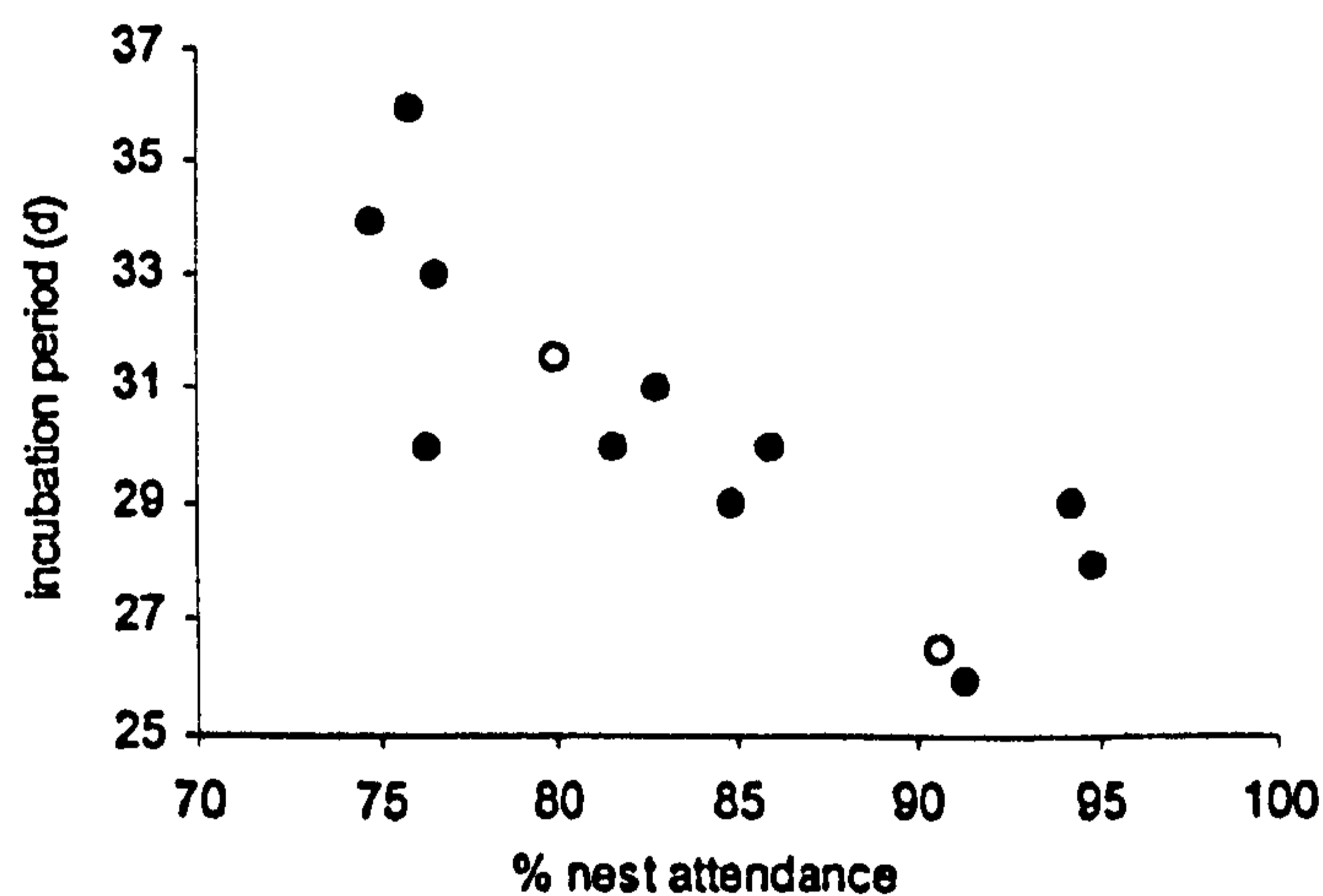


Figure 5. The relationship between incubation period duration and percentage nest attendance in dotterel. Open circles represent nests where the first egg date was estimated from pair behaviour (these two nests not included in Spearman rank correlation,  $r_s = -0.86$ ,  $N=11$ ,  $P=0.001$ )

#### Could dotterel embryos survive egg neglect?

Dotterel at 65% of 46 logged nests were absent from the nest for at least one period of more than two hours. This is probably an underestimate since only an estimated mean of 52% of the full incubation period was logged per nest. 57% of the 30 nests with nest absences of more than two hours hatched at least one chick. None of the 13 nest failures where there were long absences could be attributed definitely to egg chilling. Five failed because of trampling, three through depredation, and five through desertion. One of the deserted

clutches was abandoned during hatch. Another of the deserted clutches was abandoned only when hatch was long overdue and the eggs contained no visible embryos: the eggs may have been infertile or the embryos may have died early in incubation. Of the nests with long absences that only partially hatched, one had eggs trampled, one contained an inviable egg with no visible embryo, and three either died during hatching or were abandoned in the nest when the rest of the brood left. Data on long trips for the 17 nests that hatched after nest absences of at least two hours are summarised in Figs 6-9. Embryos that experienced long and frequent periods of chilling to low temperatures, even up to the point of hatch, were able to hatch and fledge (Figs. 6-9). The mean shaded air temperatures during the 126 absences of more than two hours was 3.3°C (range 0.0 to 12.6°C). Ground temperature was a mean of  $1.2 \pm 0.3^\circ\text{C}$  (95% C.L.) warmer than air temperature in the 116 long trips when both were recorded. At the ambient temperatures during long trips, embryonic metabolism would be unlikely to have any effect on egg temperature (Mathiu et al. 1994). Long trips were almost all made in poor weather conditions without intense solar radiation. Hence, shaded air temperature should reasonably accurately reflect equilibrium egg temperature during long trips.

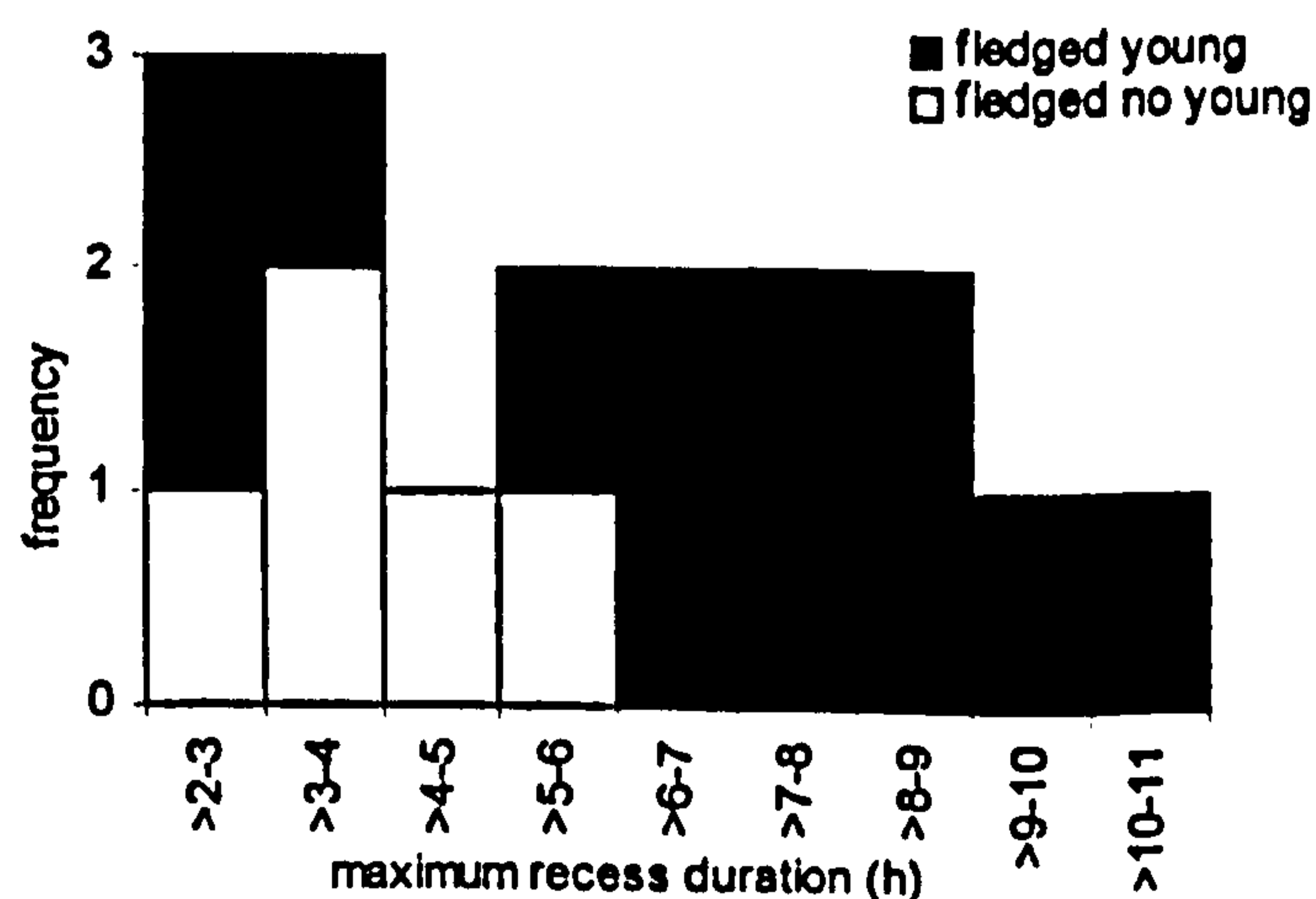


Figure 6. Maximum trip length for 17 nests that hatched at least one chick and had one or more trips of more than two hours

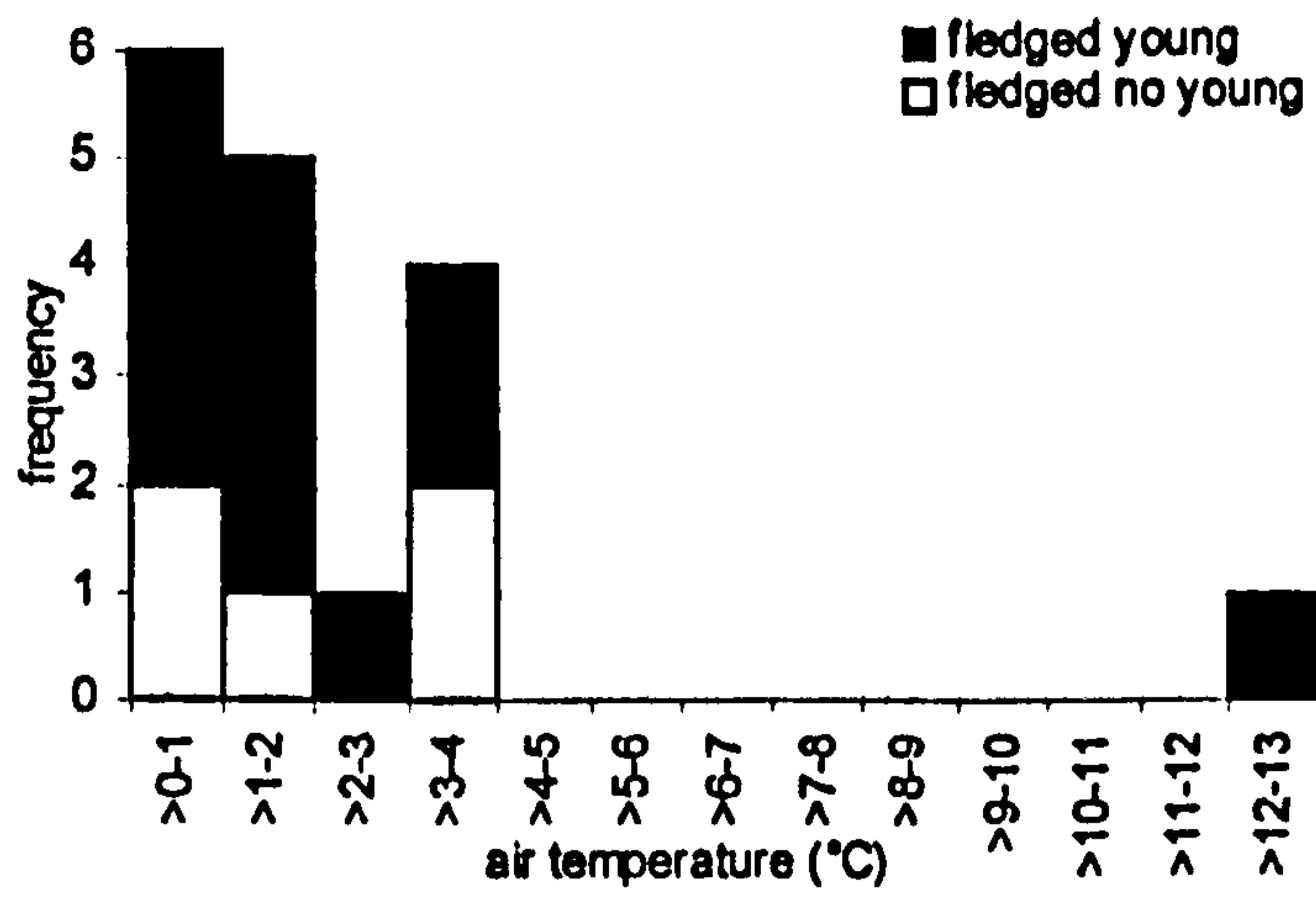


Figure 7. The minimum mean shaded air temperature per nest during trips of at least two hours from 17 nests that hatched at least one chick

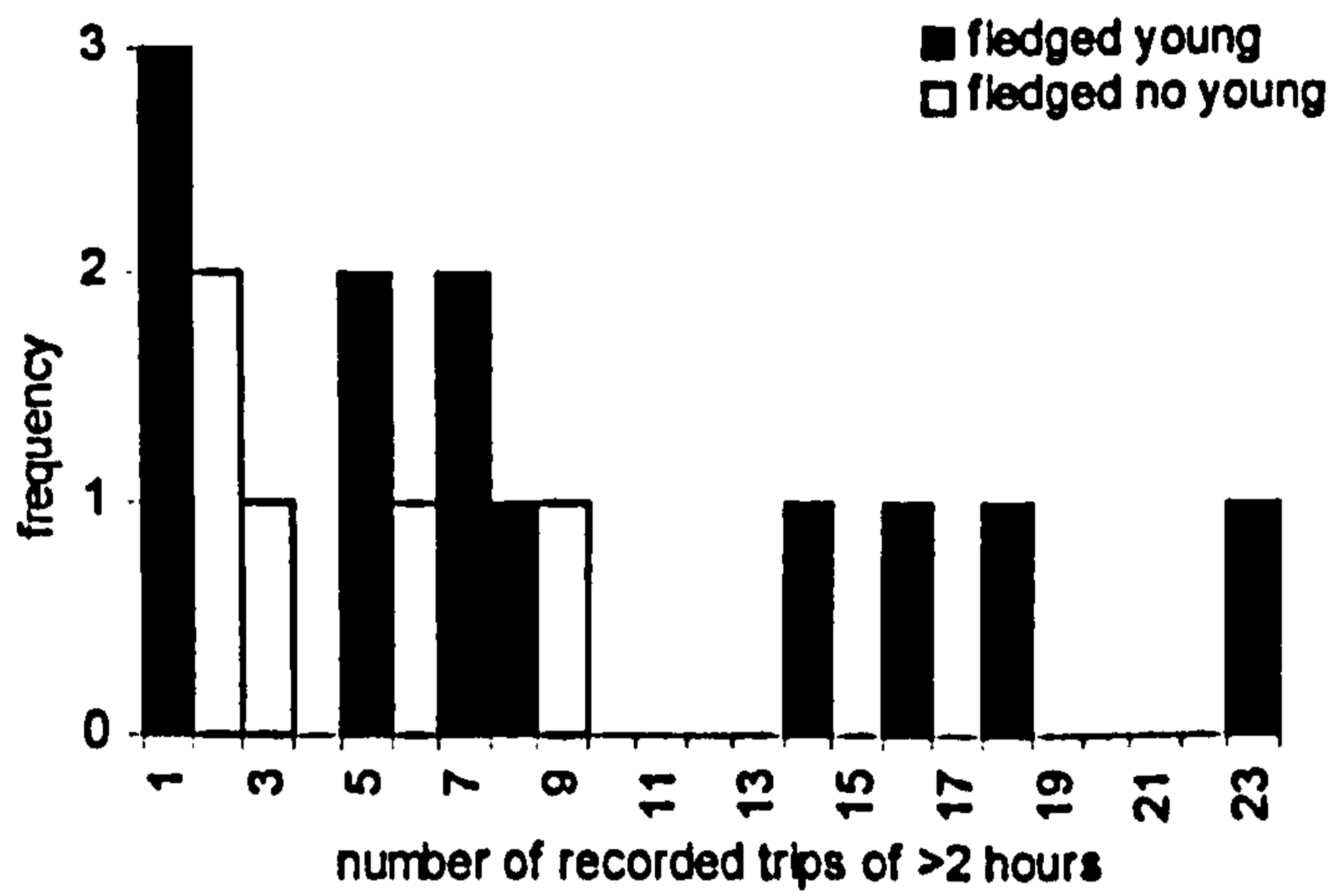


Figure 8. The number of trips of at least two hours made for 17 nests that hatched at least one chick

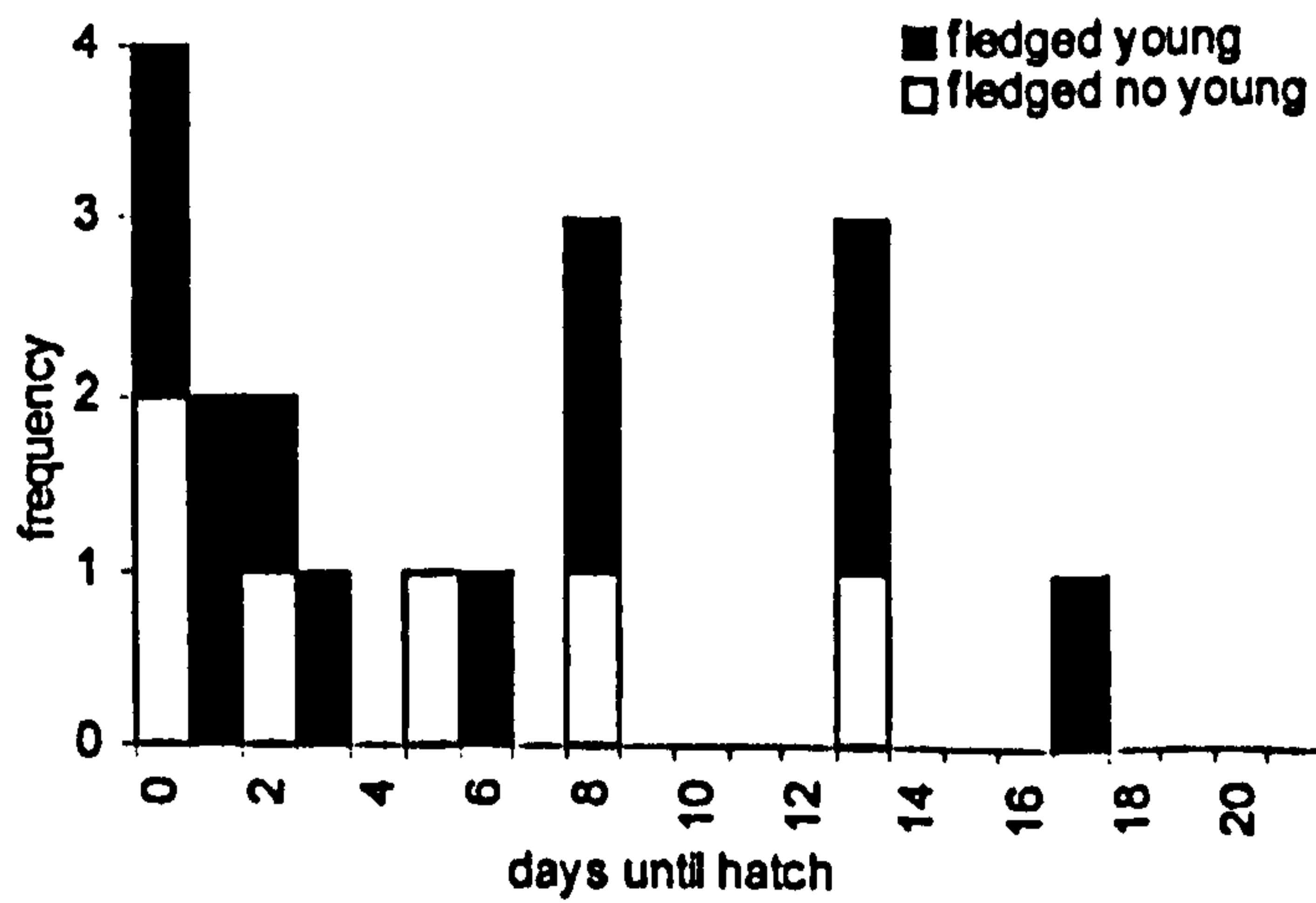


Figure 9. Histogram of the minimum number of days until hatch per nest that a trip of at least two hours was made, for 17 nests that hatched at least one chick

## DISCUSSION

Uniparental dotterel's nests were attended less and neglected more frequently than biparental nests and, in less favourable conditions, single parents further reduced their nest attendance and increased their rate of egg neglect. However, dotterel embryos were able to survive numerous long periods of neglect at low temperatures, even close to hatch (see also Pulliainen & Saari 1994). In a cool alpine climate, a parent's average energetic costs are likely to be high and when costs increase or food availability decreases in poor weather, a uniparental incubator may be forced to spend long periods feeding away from the nest (Chapter 3). An ability to successfully neglect the eggs may be a prerequisite for uniparental intermittent incubation in an energetically demanding or unpredictable climate.

Although dotterel embryos could survive neglect, there was a cost to reduced nest attendance: nests that were attended less took longer to hatch. Using the mean value of 0.974 for the daily probability of clutch survival in Scotland (D.P. Whitfield unpublished data), a clutch with the shortest sample incubation period of 26 days has a 50% probability of surviving to hatch, whereas a clutch with the longest incubation period of 36 days has only a 38% probability (Mayfield 1961). Extended incubation periods will have implications for hatching success whenever the probability of failure is a function of exposure time (Martin 1987; reviewed in Williams 1996). Additionally, extended incubation periods may leave the parent in poorer body condition (Siikamaki 1995; Tombre & Erikstad 1996) and late hatched young may have lower survivorship (e.g. Perrins 1965; Arcese & Smith 1985).

Although we found a strong relationship between incubation period duration and nest attendance, there are clearly other sources of variation in incubation period. Nest attendance may only poorly estimate the amount of time that embryos spend below the PZT if the pattern of incubation scheduling varies between nests. The eggs of a dotterel that makes many short feeding trips will spend less time below the PZT than the eggs of a dotterel that makes fewer,

longer trips of the same total duration (Haftorn 1988). In addition, clutch size (Siikamaki 1995; Hötter 1998), stage in the season (MacRoberts & MacRoberts 1972; Parsons 1972; Murphy 1995; Feldheim 1997; Hötter 1998), habitat quality (Sanz 1995) and egg size (Parsons 1972; Drent 1975; Bryant 1975) may affect incubation period duration.

The embryos of most species are thought to be killed or harmed by relatively short periods of chilling (Webb 1987) but there are few published data for shorebirds. We cannot distinguish whether the dotterel embryos' high chilling tolerance is a specific adaptation of dotterel to uniparental incubation in an alpine climate, or whether it is a characteristic of their taxon and Cartar & Montgomerie (1985) suggest that shorebirds may often have chilling tolerant eggs. There is wide variation in the parental care systems of shorebirds (Székely & Reynolds 1995) and many uniparental shorebirds breed at high latitudes where egg-chilling will be a threat (Whitfield & Tomkovich 1996; Reynolds & Székely 1997). Norton (1972) recorded high chilling tolerance in pre-incubation dunlin eggs and found that incubation, once commenced, was 'erratic and desultory' with frequent long absences at some nests. There was some indication that poorly attended dunlin nests, however, may have had lower hatching success. While Webb (1987) concluded that avian embryo chilling tolerance is low, there are anecdotal accounts of embryos from several taxa surviving long exposure to low temperatures (e.g. Semenov-Tyan-Shanskii & Bragin 1969; probably Drent 1970; Norton 1972; reviewed in Cartar & Montgomerie 1985; Haftorn 1988; Williams 1996; Sockman & Schwabl 1998). Like the data presented here, these anecdotal accounts may be biased towards chilling tolerant individuals.

Experiments investigating embryo thermal tolerance found that, rather than all embryos dying under the same sets of conditions, the proportion of embryos that died increased with the duration or degree of chilling (MacMullan & Eberhardt 1953; Batt & Cornwell 1972), indicating that embryo chilling tolerance varies within species (Webb 1987). This means that our observational data on the chill-tolerance of dotterel eggs must be treated with some caution. Seventeen of the nests that experienced long exposures successfully hatched but 13 did not. While there was no evidence that any of these failures was due to egg chilling (the single

dead clutch was infertile or ceased development prior to the start of logging), it is possible that the two mid-season desertions on eggs were due to the parents' assessments that they had damaged the eggs through neglect. However, if parents are able to assess the time taken for damaging embryo chilling to occur, then they should not return to the nest after the fatal trip and it would go unrecorded. The lowest mean and minimum shaded air temperatures recorded during long trips were 0.0°C and -0.9°C, respectively, both above the egg freezing point of about -2°C, when damage from ice crystals occurs (Wilson 1991). Cold conditions that might preclude egg neglect rarely occurred: using a model of the effect of weather variables on unattended egg temperature (Chapter 3), we estimated that if eggs were permanently unattended during the periods when birds were incubating, they would spend only between 0.5% and 1.0% of the time at or below -2°C during the four site-years. Although dotterel embryos can survive to hatch and fledge after repeated long periods of chilling to low temperatures, they may then have reduced survival or reproductive success in later life (Webb 1987).

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#### REFERENCES

Arcese, P. & Smith, J.N.M. 1985. Phenotypic correlates and ecological consequence of dominance in Song Sparrows. Journal of Animal Ecology, 54, 817-830.



- Batt,B.D. & Cornwell,G.W. 1972. The effects of cold on Mallard embryos. Journal of Wildlife Management , 36, 745-751.
- Boersma,P.D. 1982. Why some birds take so long to hatch. American Naturalist , 120, 733-750.
- Boersma,P.D. & Wheelwright,R.D. 1979. Egg neglect in the Procellariiformes: reproductive adaptation in the Fork-tailed Storm-petrel. The Condor , 81, 157-165.
- Bryant,D.M. 1975. Breeding biology of House Martins *Delichon urbica* in relation to aerial insect abundance. Ibis , 117, 180-216.
- Cartar,R.V. & Montgomerie,R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour , 95, 261-289.
- Chaurand,T. & Weimerskirch,H. 1994. Incubation routine, body-mass regulation and egg neglect in the Blue Petrel *Halobaena caerulea*. Ibis , 136, 285-290.
- Cramp,S. & Simmons,K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic: Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Drent,R.H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Supplement , 17, 1-132.
- Drent,R.H. 1975. Incubation. In: Avian Biology (Ed. by D.S.Farner & J.R.King), pp. 333-420. New York: Academic Press.
- Drent,R.H., Tinbergen,J.M. & Biebach,H. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands Journal of Zoology, 35, 103-123.
- Feldheim,C.L. 1997. The length of incubation in relation to nest initiation date and clutch size in dabbling ducks. The Condor , 99, 997-1001.
- Haftorn,S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Ornis Scandinavica, 19, 97-110.
- Holt,S., Whitfield,D.P., Duncan,K., Rae,S. & Smith,R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? Journal of Avian Biology , 33, 219-224

- Horsfield,D. & Thompson,D.B. 1996. The uplands: guidance on terminology regarding altitudinal zonation and related terms. Information and Advisory Note 26. Battleby, UK: Scottish Natural Heritage.
- Hötter,H. 1998. Intraspecific variation in length of incubation period in Avocets *Recurvirostra avosetta*. Ardea , 86, 33-41.
- Johnson,D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk , 96, 651-661.
- Kálás,J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Lill,A. 1979. Nest attentiveness and its influence on the development of young of the Superb Lyrebird. The Condor , 81, 225-231.
- MacMullan,R.A. & Eberhardt,L.L. 1953. Tolerance of incubating pheasant eggs to exposure. Journal of Wildlife Management , 17, 322-330.
- MacRoberts,M.H. & MacRoberts,B.R. 1972. The relationship between laying date and incubation period in Herring and Lesser Black-backed Gulls. Ibis , 114, 93-97.
- Martin,T.E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics , 18, 453-487.
- Martin,T.E. & Ghalambor,C.K. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? American Naturalist , 153, 131-139.
- Mathiu,P.M., Dawson,W.R. & Whittow,G.C. 1994. Thermal responses of late embryos and hatchlings of the Sooty Tern. The Condor , 96, 280-294.
- Mayfield,H. 1961. Nesting success calculated from exposure. Wilson Bulletin , 73, 255-261.
- Miskelly,C.M. 1989. Flexible incubation system and prolonged incubation in New Zealand Snipe. Wilson Bulletin , 101, 127-132.
- Morton,M.L. & Pereyra,M.E. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). Auk , 102, 25-37.
- Murphy,E.C. 1995. Seasonal declines in duration of incubation and chick period of Common Murres at Bluff, Alaska in 1987-1991. Auk , 112, 982-993.
- Nethersole-Thompson,D. 1973. The Dotterel. Glasgow: Collins.

- Norton, D.W. 1972. Incubation schedules of four species of Calidrine sandpipers at Barrow, Alaska. The Condor , 74, 164-176.
- Norusis, M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Gorinchem: SPSS Ltd.
- Parsons, J. 1972. Egg size, laying date and incubation period in the Herring Gull. Ibis , 114, 536-541.
- Perrins, C.M. 1965. Population fluctuations and clutch-size in the Great Tit *Parus major* L. Journal of Animal Ecology , 34, 601-647.
- Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.
- Pulliainen, E. & Saari, L. 1994. Incubation behaviour of the Dotterel *Charadrius morinellus*. Oecologia Montana , 3, 27-34.
- Reed, A., Hughes, R.J. & Gauthier, G. 1995. Incubation behaviour and body mass in Greater Snow Geese. The Condor , 97, 993-1001.
- Reynolds, J.D. & Székely, T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. Behavioral Ecology , 8, 126-134.
- Sanz, J.J. 1995. Environmental restrictions on reproduction in the Pied Flycatcher *Ficedula hypoleuca*. Ardea , 83, 421-430.
- Semenov-Tyan-Shanskii, O.I. & Bragin, A.B. 1969. Incubation conditions for some precocial birds in the subarctic. Byulleten Moskovskogo Obshchestva Ispytatelei Prirody. Otdel. Biol. 74, 50-66.
- Slikamaki, P. 1995. Are large clutches costly to incubate? - the case of the Pied Flycatcher. Journal of Avian Biology , 26, 76-80.
- Smith, H.G., Sandell, M.I. & Bruun, M. 1995. Paternal care in the European Starling, *Sturnus vulgaris* - incubation. Animal Behaviour , 50, 323-331.
- Sockman, K.W. & Schwabl, H. 1998. Hypothermic tolerance in an embryonic American kestrel (*Falco sparverius*). Canadian Journal of Zoology , 76, 1399-1402.
- Spiers, D.E. & Baummer, S.C. 1990. Embryonic development of Japanese Quail (*Coturnix coturnix japonica*) as influenced by periodic cold exposure. Physiological Zoology , 63, 516-535.

- Székely, T. & Reynolds, J.D. 1995. Evolutionary transitions in parental care in shorebirds. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 262, 57-64.
- Tombre, I.M. & Erikstad, K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Vleck, C.M. & Kenagy, G.J. 1980. Embryonic metabolism of the Fork-tailed Storm Petrel: physiological patterns during prolonged and interrupted incubation. Physiological Zoology, 53, 32-42.
- Webb, D.R. 1987. Thermal tolerance of avian embryos: A review. The Condor , 89, 874-898.
- Whitfield, D.P. & Tomkovich, P.S. 1996. Mating system and timing of breeding in holarctic waders. Biological Journal of the Linnean Society , 57, 277-289.
- Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Williams, J.B. 1996. Energetics of avian incubation. In: Avian energetics and nutritional ecology (Ed. by C.Carey), pp. 375-415. New York: Chapman & Hall.
- Wilson, H.R. 1991. Physiological requirements of the developing embryo: temperature and turning. In: Avian Incubation (Ed. by S.G.Tullet), pp. 145-156. Rushenden, U.K.: Butterworth-Heinemann Ltd.

## **Chapter 5**

### **DO INCUBATING EURASIAN DOTTEREL ORIENT INTO THE WIND?**

Sue Holt, D. Philip Whitfield & David M. Bryant

#### **ABSTRACT**

Incubating dotterel oriented themselves frontwards into the wind while sitting on the nest and their probability of orienting into the wind increased with the wind speed.

## INTRODUCTION

The energetic cost of thermoregulation for shorebirds breeding in arctic-alpine conditions can be very high (Wiersma & Piersma 1994; Piersma & Morrison 1994) so that birds may frequently exceed their hypothetical metabolic ceiling (Piersma & Morrison 1994; Drent & Daan 1980) or suffer non-adaptive mass loss (S.Holt et al. unpublished data). Any behaviour that reduces this energetic cost may increase the individual's fitness by increasing the probability of the current breeding attempt succeeding or of the parent surviving and successfully breeding again (Monaghan & Nager 1997; Thomson et al. 1998). Roosting shorebirds often orient the front of their bodies into the wind (e.g. Hale 1980; Wiersma 1991; Ferns 1992). This is likely to reduce their energetic costs of thermoregulation as the feathers are less likely to be ruffled, which would disrupt the insulating air trapped within the plumage, increasing the birds thermal conductance (Goldstein 1983; Wiersma 1991, although measurements were made using a heated taxidermic mount and live birds may have some control of feather position; Wiersma et al. 1993). The magnitude of this potential increase in the energetic cost of thermoregulation indicates that behavioural adaptations to prevent wind penetration into the plumage will be subject to strong selective pressure (Walsberg 1986). In addition, the greater streamlining of orienting frontward into the wind may reduce the energy a shorebird has to expend to remain standing against the force of the wind or reduce the possibility of injury through being pushed along or over. While wintering shorebirds are well known to orient into the wind there is little published quantitative data for breeding shorebirds sitting on their nests. In Scotland, the Eurasian dotterel *Charadrius morinellus* breeds in the alpine zone of the highest hills, where the dwarf vegetation provides little shelter from the characteristically high wind speeds (S. Holt et al. unpublished data). In this study we test whether incubating Eurasian dotterel *Charadrius morinellus* orient themselves into the wind.

As well as minimising the costs of thermoregulation and reducing buffeting, orienting into the wind may have a third advantage: like many shorebirds, incubating dotterel rely partly on their crypsis to prevent predation of their eggs and feathers flapping in the wind may increase their conspicuousness (the scapular feathers of incubating dotterel were seen flapping on three

occasions when not facing directly into the wind at Beaufort Scale wind scores of more than three, pers. obs). We attempt to distinguish whether one functional explanation for orientation into the wind is the reduction of the energetic cost of thermoregulation by testing whether dotterel were more likely to orient into the wind when it was colder and the effect of the increased conductance of ruffled plumage on the cost of thermoregulation would be greater.

Incubating birds may orient themselves into the wind by either changing their sitting direction in response to current wind direction or by having a fixed direction or directions that will orient them into the prevailing wind directions. Charadriiformes may orient themselves in the direction that they arrive at their nest from a favoured approach route (Baerends et al. 1970). Dotterel also appear to have a small number of favoured approach routes to the nest and often initially sit according to how they arrived at the nest (pers. obs.). However, especially in favourable weather conditions, dotterel frequently stand up and resettle facing in a new direction, often within a few minutes of arriving at the nest (pers. obs.). We attempt to test whether the mechanism for orientation into the wind is the use of favoured sitting directions that orient into the prevailing wind or a response to current conditions, by testing whether dotterel were more likely to face into the prevailing wind directions even at low wind speeds.

## **METHODS**

Data on the orientation of sitting birds were collected from 78 nests on sites B and D between 1990 and 1998. Dotterel are vulnerable to illegal egg collectors so site names are not given. When a nest was checked to monitor breeding success, the compass direction the sitting dotterel's head was facing was recorded (to the nearest 45°, i.e. N, NE, E, SE, S, SW, W and NW). The direction of the wind, and the wind speed estimated on the Beaufort scale, were also recorded. Comparison of Beaufort wind speed estimates and wind speed measures from a Kestrel hand-held anemometer (Nielson-Kellerman, Chester, USA) showed that Beaufort scale wind scores were consistently underestimated. Data are presented as scored in the

field, but a calibration of these scores to the Beaufort Scale and measured wind speed is also given (Table 1).

Table 1. Wind speed score, equivalent Beaufort Scale score, and mean wind speed measured at 1.45m above ground level using a handheld anemometer.

wind speed score	mean wind speed at 1.45m above ground level, ms <sup>-1</sup>	equivalent Beaufort Scale score
0	0.0	0
1	1.9	1-2
2	3.8	3
3	6.0	4-5
4	8.5	6
5	10.0	7
6	12.9	8

Nests each contributed a mean of 4.9 data points but only one datum was used per nest to avoid pseudoreplication. Statistical tests were carried out using SPSS (Norusis 1990). Two-tailed probabilities are given. Means are quoted  $\pm$  95% confidence limits.

## RESULTS

Dotterel faced into the wind significantly more than expected at all wind speeds recorded (Table 2, Fig. 1).



Table 2. The proportion of sitting birds facing directly into the wind (one randomly selected datum per wind speed per nest). The expected proportion of birds facing into the wind was 0.125, based on eight recorded compass bearing. G-test statistics are given with William's corrections, *d.f.*=1. Using sequential Bonferoni (Rice 1989) for multiple tests, all test probabilities remain significant to  $P < 0.001$  ( $k=4$ ).

wind speed score	<i>n</i> facing into wind (% facing into wind)	<i>n</i> facing in other directions	$G_{adj}$	<i>P</i>
1	16 (44%)	20	22.115	<0.001
2	17 (40%)	25	20.443	<0.001
3	36 (67%)	18	84.996	<0.001
4	22 (69%)	10	expected cell counts of less than 5	
5	12 (75%)	4		
6	5 (83%)	1		
4, 5 & 6	39 (72%)	15	101.452	<0.001

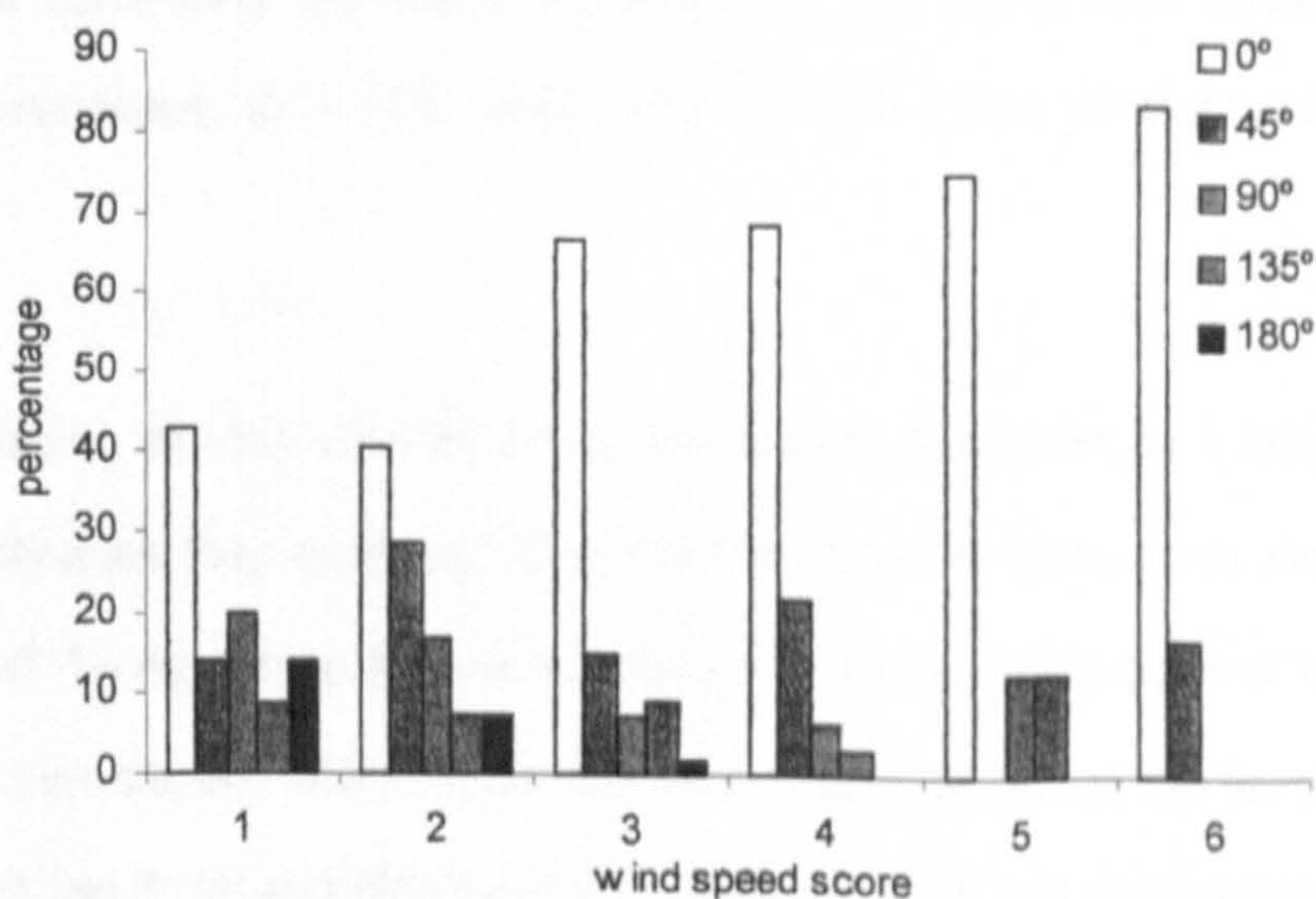


Figure 1. The difference between wind direction and dotterel orientation at different wind speeds (one datum per wind speed per nest).

The proportion of dotterel facing into the wind increased with wind speed (Spearman's rank correlation:  $r_s=0.886$ ,  $n=6$ ,  $P=0.019$ , one randomly selected datum used per nest, Fig. 2).

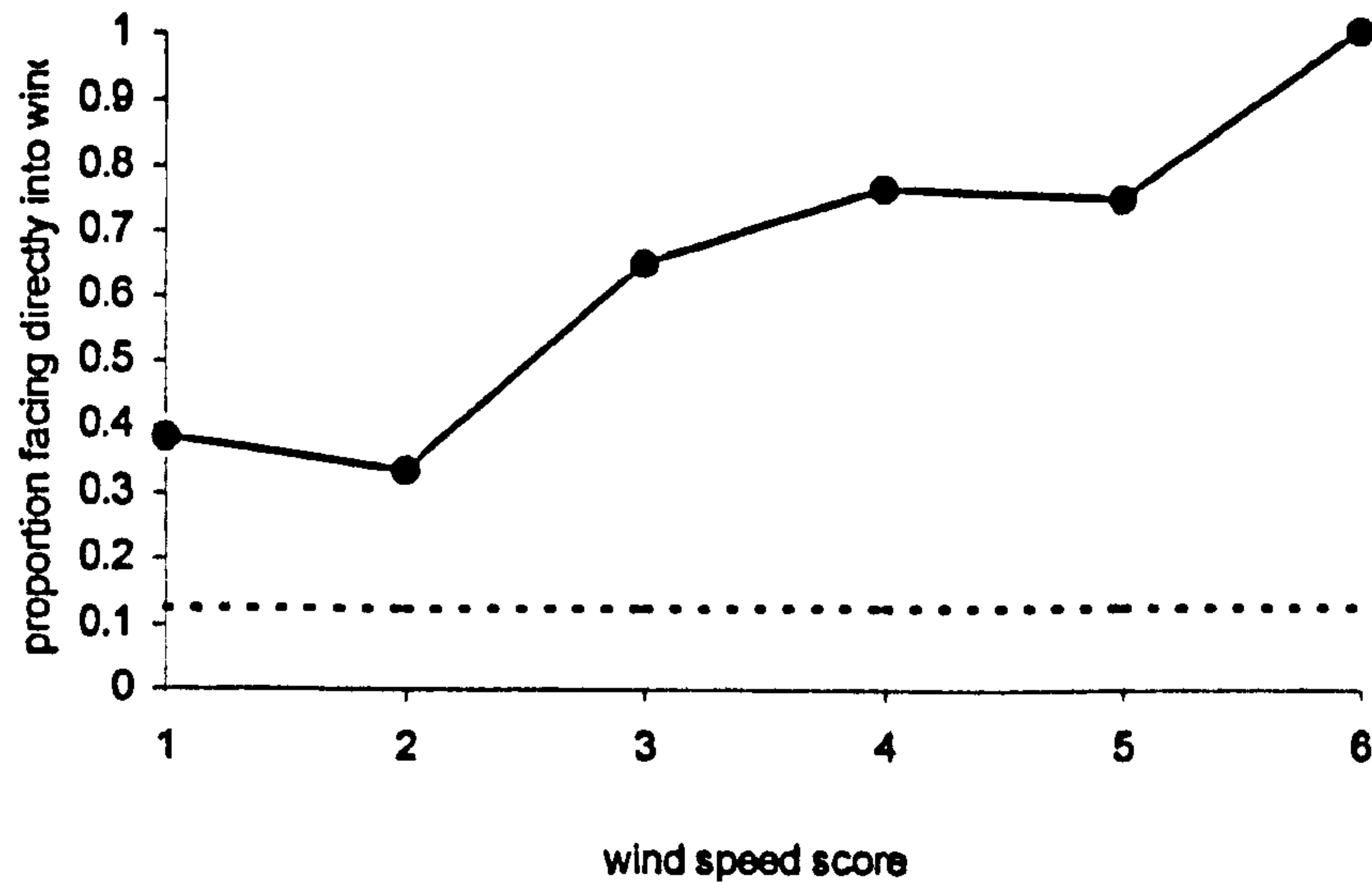


Figure 2. The proportion of incubating birds facing into the wind (one datum per nest). The dashed line shows the expected proportion of birds facing directly into the wind if they oriented independently of wind direction (0.125, based on eight compass bearings).

We found no evidence that dotterel were more likely to face directly into the wind when it was colder (sign-test comparing the same individuals at the same wind speed at cooler and warmer air temperatures:  $Z=-1.000$ ,  $N=20$ ,  $P=0.317$ , the mean temperature difference was  $3.8^{\circ}\text{C}$ )

Do dotterel sit facing into the wind because they orient themselves as a response to current conditions, or because they generally face into the direction from which strong winds most frequently come? To determine this we looked at the sitting orientations of birds at low wind speeds. Winds from the NE and E occur the least frequently and at the lowest mean speeds while winds from the S, W and NW have the highest speeds and frequencies (Fig. 3), so we tested whether, at wind speed scores of zero or one, dotterel face S, W or NW more frequently than they face NE or E.

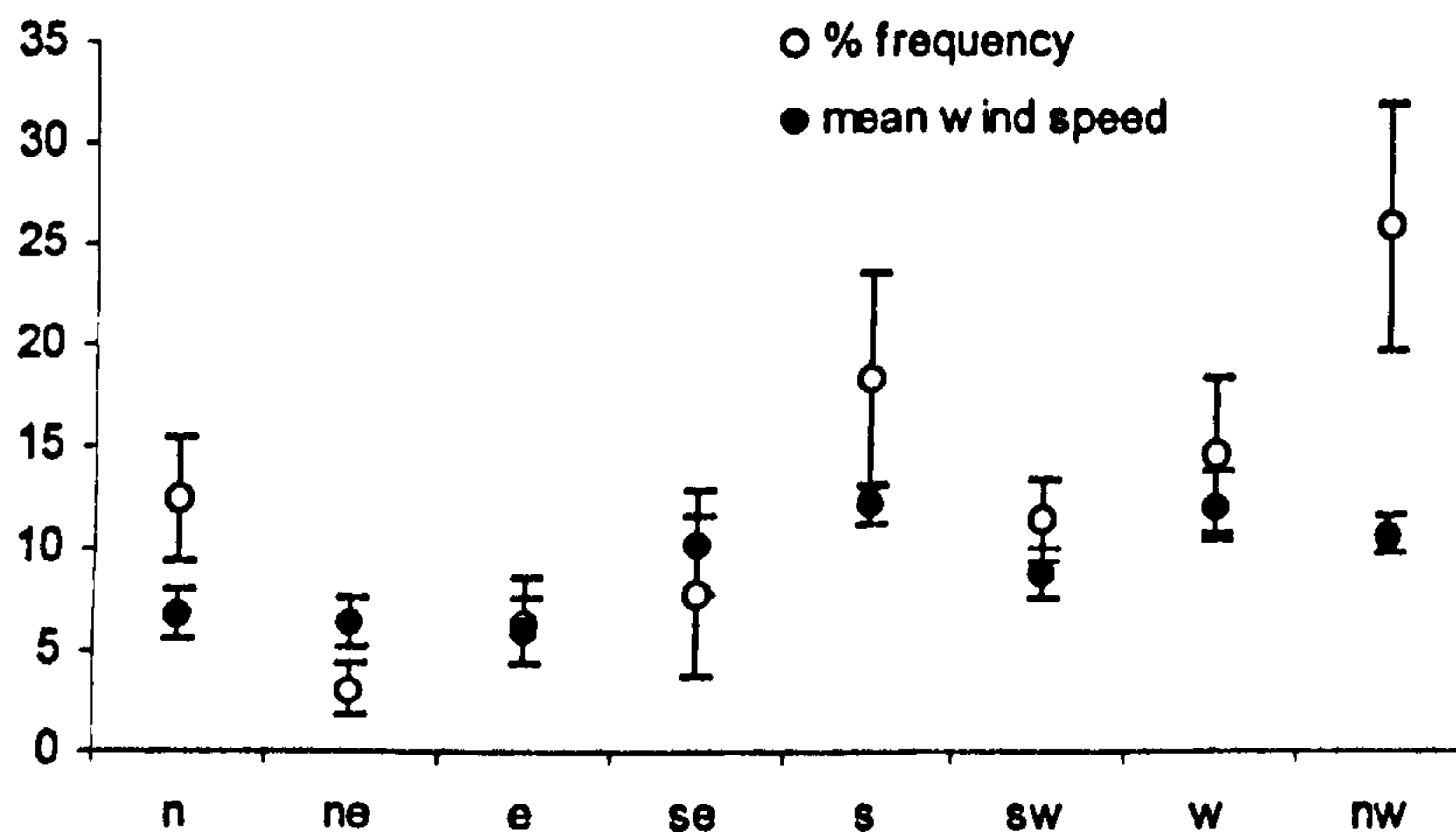


Figure 3. The frequency and speed of wind from different directions recorded by the Automatic Weather Station on Cairn Gorm summit at 4m above ground level, approximately 40km from sites B and D (confining data to the six years between 1990 and 1999, inclusive, when there were wind speed data for at least 60% of the range of Julian dates that included 95% of the sample dates on which dotterel incubated, extrapolating from first egg dates)

At low wind speeds dotterel did not face S, W or NW more frequently than NE or E than the 3:2 ratio expected by chance (G-test with William's correction:  $G_{s,df}=0.563$ ,  $df=1$ ,  $P=0.454$ , six records of birds facing either NE or E and 13 cases of birds facing S, W or NW, one datum per nest).

Did dotterel fail to orient into the wind on all occasions because they had a small set of sitting directions? When not oriented into the wind dotterel sat in a significantly smaller number of different directions than expected from chance (one-sample t-test comparing the number of different sitting directions in five randomly selected records per nest with the expected number of directions calculated from 25500 simulations:  $t_{12}=2.404$ ,  $P=0.033$ , observed number of different directions  $3.4 \pm 0.4$ , expected number  $3.9 \pm 0.0$ ). However, dotterel were clearly not confined to a narrow set of directions as, from those nests with at least five records, birds were recorded sitting in a mean of 5.0 (range three to eight) different directions.

## DISCUSSION

Dotterel oriented frontward into the wind and their probability of facing into the wind increased with wind speed. Cartar & Montgomerie (1985) review data for other breeding shorebirds that face into the wind and thought that incubating white-rumped sandpipers *Calidris fuscicollis* faced winds of more than  $5\text{ms}^{-1}$  measured at 2m above ground level (equivalent to over our wind speed score of 2 after correcting for the anemometer height above ground using a standard logistic equation, HMSO 1982).

We could not clearly distinguish either the mechanism or functional explanation for orientation into the wind. We tried to determine whether minimising the energetic cost of thermoregulation was an appropriate functional explanation by testing whether the same individual birds were more likely to orient into the wind at lower air temperatures, when the increase in the thermal conductance of ruffled plumage would have a greater effect on energetic costs. We found no evidence that birds were likely to orient into the wind when it was colder, but we had little power to test the hypothesis as both the sample size and the variation in temperature were small. Similarly, we found no evidence that dotterel were more likely to orient in the prevailing wind directions at low wind speeds, suggesting that dotterel adjust their orientation according to current weather conditions rather than favouring the prevailing wind direction regardless of wind speed. Our sample was small, however, giving us little power to reject the latter mechanism.

Although we found that dotterel chose to orient into the wind more frequently than expected by chance, even at higher wind speeds they oriented in other directions in 28% of cases. Microhabitat features such as graminoid tussocks or hummocks can reduce the speed of wind experienced at the nest (S. Holt et al. unpublished data), so that a dotterel apparently facing away from a strong wind may actually be experiencing a low local wind speed. Dotterels' orientation on the nest may be influenced by factors other than wind. Orientation may affect not only the rate of heat loss through forced convection but also the rate of heat gain from insolation, especially in birds whose contrasting plumage colours give variation in radiation

absorption depending on orientation (Elkins 1983; references in Wiersma 1991, Walsberg, G.E. 1993): dotterel may not orient into the wind if they can gain more from solar heating than they lose from the increased rate of convection. It may be important for birds to vary their orientation on the nest to ensure that their entire clutch is adequately warmed (Baerends et al. 1970), so that birds may forfeit orientation into the wind to maintain their embryos' thermal environment. The view of approaching predators varies with microhabitat features (S. Holt et al. unpublished) so dotterel may choose to orient away from features that obscure their view. Alternatively, dotterel sometimes at least initially sit in the direction that they arrived at the nest from a preferred approach route (pers. obs.). Dotterel did not appear to be confined to a narrow set of directions but they sat in fewer directions than expected from chance, suggesting preference for some directions.

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## **REFERENCES**

- Baerends, G.P., Drent, R.H., Glas, P. & Groenewold, H. 1970. An ethological analysis of incubation behaviour in the Herring Gull. *Behaviour Supplement* 17, 135-234.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour* 95, 261-289.
- Drent, R. H. and Daan, S. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68, 225-252.

Elkins, N. 1983. *Weather and Bird Behaviour*. Waterhouses, Staffordshire, U.K.: T & A D Poyser.

Ferns, P.N. 1992. *Bird Life of Coasts and Estuaries*. Cambridge: Cambridge University Press.

Goldstein, D. L. 1983. Effect of wind on avian metabolic rate with particular reference to Gambel's Quail. *Physiological Zoology* **56**, 493-505.

Hale, W.G. 1980. *Waders*. London: Collins.

HMSO 1982. *Observer's Handbook*. 4th edn. London: HMSO.

Monaghan, P. & Nager, R.G. 1997. Why don't birds lay more eggs? *Trends In Ecology & Evolution* **12**, 270-274.

Norusis, M.J. 1990. *SPSS/PC+ Advanced Statistics 4.0*. Gorinchem: SPSS Ltd.

Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. *Auk* **111**, 366-376.

Rice, W.R. 1989. Analysing tables of statistical tests. *Evolution* **43**, 223-225.

Thomson, D.L., Monaghan, P. & Furness, R.W. 1998. The demands of incubation and avian clutch size. *Biological Review* **73**, 293-304.

Walsberg, G. E. 1986. Thermal consequences of roost site selection: the relative importance of three modes of heat conservation. *Auk* **103**, 1-7.

Walsberg, G. E. 1993. Thermal consequences of diurnal habitat selection in a small bird. *Ornis Scandinavica* **24**, 174-182.

Wiersma, P. 1991. Living Exposed and in the Cold. Thermostatic Costs of Nearctic Knots (*Calidris canutus islandica*) As Measured by Means of Heated Taxidermic Mounts. Masters thesis: University of Groningen

Wiersma,P., Bruinzeel,L. & Piersma,T. 1993. Energy savings in waders: Studies on the insulation of Knots. *Limosa* 66, 41-52.

Wiersma,P. & Piersma,T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. *The Condor* 96, 257-279.

## Chapter 6

### DOES FINE-SCALE NEST SITE SELECTION IN THE EURASIAN DOTTEREL MINIMIZE ENERGETIC COSTS OR PREDATION RISK?

Sue Holt, D. Philip Whitfield & David M. Bryant

#### ABSTRACT

In this study we investigated the fine-scale nest site selection of the Dotterel (*Charadrius morinellus*). At a fine spatial scale, dotterel selected deep vegetation for nest sites. Nests in deeper vegetation had more nest lining and the eggs sat further below ground level, probably reducing the parents' energetic costs of incubation and improving the eggs' thermal environment. Although wind is an important determinant of the high thermoregulatory costs in shorebirds, dotterel did not select nest sites that minimized their exposure to wind. Early detection of potential predators may allow individuals to make more effective responses to predators but dotterel did not select nest sites that gave better visibility, at any spatial scale tested. They did, however, at a very local scale select nest sites that were more heterogeneous than the surrounding habitat. More heterogeneous habitat may make sitting dotterel and their exposed eggs less conspicuous to predators that search visually.



## INTRODUCTION

'A good nest in a good place is the key to breeding success for many birds' (Collias & Collias 1984). In support of this statement, numerous studies have found that the probability of nesting failure can vary with nest construction (Møller 1987; Møller 1989; Byrkjedal & Thompson 1998) or nest site characteristics, such as concealment from or accessibility to predators (Nias 1986; Martin & Roper 1988; Rands 1988; Petersen 1990; Tuomenpuro 1991; Ille et al. 1996; Regehr et al. 1998; Halupka 1998; Stokes & Boersma 1998; Hooge et al. 1999), height above the ground (Osborne & Osborne 1980; Nias 1986; Martin 1988; Seitz & Zegers 1993; Sockman 1997; Ford 1999), microclimate (Austin 1974; Osborne & Osborne 1980; Wachob 1996; Halupka 1998; Stokes & Boersma 1998; Hooge et al. 1999), local abundance of similar nesting habitat (Joern & Jackson 1983; Martin & Roper 1988; Tarvin & Smith 1995) and proximity to human structures (Osborne & Osborne 1980; Tarvin & Smith 1995). Selection will favor individuals which choose nest sites that maximize the probability of their own and their eggs' survival.

Clutch predation is often a main cause of nesting failure (Ricklefs 1969) and parents are sometimes depredated while incubating (e.g. Soikkeli 1967). Birds should, therefore, select nest sites that minimize their own and their eggs' risk of predation. Having good visibility of approaching predators may allow parents to identify the risk represented by the predator early and then to take the best action for survival of themselves or their eggs (Götmark et al. 1995; Byrkjedal & Thompson 1998), especially as the optimal response can differ between predators (Buitron 1983). Shorebirds' visibility of approaching predators, and the nature and effectiveness of their nest defense response, can vary with characteristics of the nest site (Colwell & Oring 1990; Koivula & Ronka 1998).

The Eurasian dotterel *Charadrius morinellus* is a shorebird that breeds in the Arctic-Alpine zones of the Palearctic. A significant proportion of dotterel clutches are lost to predators (a mean of 18% in Scotland, 47% in a Norwegian population and 5% in a Finnish study, D. P. Whitfield unpublished data; Byrkjedal 1987; Pulliainen & Saari 1992b) so that variation in

parents' risk of clutch predation will have fitness implications. Dotterel nest on the ground in dwarf plant communities that are often broken by freeze-thaw hummocks or peat hags and scattered with patches of taller graminoid tussocks. An incubating dotterel's visibility of approaching predators may be obscured by tussocks, hummocks, or larger scale topography. Dotterel's flushing distances vary greatly between and within individuals (Pulliainen & Saari 1995; Chapter 7) and may vary with predator species (Wilkie 1980). We test the hypothesis that dotterel select nest sites with better visibility that allow earlier predator detection.

The conspicuousness of a dotterel's nest is likely to be an important determinant of hatching success as avian predators that hunt visually take a significant proportion of clutches (Cramp & Simmons 1983; Byrkjedal 1987; Pulliainen & Saari 1992b; Holt & Whitfield 1996a; Holt & Whitfield 1996b; Holt & Whitfield 1996c; D.P. Whitfield unpublished). Shorebirds often site their nests near conspicuous objects or on disruptive substrates where they and their exposed eggs may be less conspicuous (Maclean & Moran 1965; Nethersole-Thompson 1973; Graul 1975; Nethersole-Thompson & Nethersole-Thompson 1981; Colwell & Oring 1990). Accordingly, we tested whether dotterel sited their nests on heterogeneous ground as such locations should reduce the risk of a visual predator finding nests.

The microclimate of a nest site can affect breeding success (Austin 1974; Austin 1976; Halupka 1998; Hooge et al. 1999) and some species, especially those breeding in very cold or hot environments, choose nest sites that provide a favorable microclimate (Calder 1973b; Austin 1974; Austin 1976; Zerba & Morton 1983; Collias & Collias 1984; With & Webb 1993; Gloutney & Clark 1997; Halupka 1998; Hooge et al. 1999; Nelson & Martin 1999). The energetic costs of thermoregulation and incubation in dotterel's cool, windy and wet Alpine habitat are probably relatively high, as in high latitude shorebirds (Piersma & Morrison 1994; Andreev 1999). As most dotterel nests are incubated by the male alone (Cramp & Simmons 1983), all costs are borne by a single individual with limited foraging time (Kálás 1986) and dotterel sometimes lose mass through energetic shortfall during incubation (S. Holt et al. 2002; Kálás & Byrkjedal 1984; Pulliainen & Saari 1992a). To increase the chances of clutch survival and/or maintain body condition, dotterel should therefore select nest sites that

minimize their energetic costs during incubation. Wind speed is an important determinant of shorebirds' high costs of thermoregulation and the wind speeds that birds experience vary with habitat structure (Wiersma & Piersma 1994; Piersma & Morrison 1994). We tested whether dotterel chose nest sites that minimized their exposure to wind.

Dotterel hollow their open nest cup out of the vegetation layer and then line the cup with plant materials (Cramp & Simmons 1983). The depth of the vegetation in which a dotterel nest is sited may affect the microclimate inside the nest, as the depth of the nest cup is likely to be constrained by the depth of vegetation overlying the harder substrates of soil, stone or gravel. A deep nest cup may give room for more nest lining, which may reduce the rate of heat loss from the eggs to the ground and so reduce the cost of incubation (Collias & Collias 1984). A deeper cup may also allow the eggs to sit further below the ground surface. This may reduce the wind speed and cooling rate that exposed eggs experience, thereby reducing the parent's cost of re-warming and the time eggs spend below a temperature suitable for development. We investigated whether deeper vegetation is likely to improve nest microclimate by analyzing the relationship between vegetation depth and nest parameters, and we tested whether dotterel sited their nests in deeper vegetation.

Animals may select habitat features at a variety of spatial scales but many studies of habitat selection only investigate selection at a single spatial scale (Orians & Wittenberger 1991; Pribil & Picman 1997). When animals choose habitat characteristics at a variety of spatial scales, it is important that sampling is at an appropriate scale if an insight into habitat preferences is to be gained. For example, Pribil & Picman's (1997) study of nest site selection at two spatial scales found that nesting Red-winged Blackbirds, *Agelaius phoeniceus*, selected dense stands of cattail *Typha*, surrounded by low density cattail: hence comparison of nest sites only to the larger scale would have revealed no selection with respect to cattail density. The scale at which habitat characteristics vary may also affect perceived habitat selection: for example, if an animal prefers a certain characteristic that only varies on a large spatial scale, studies that test for habitat selection within a smaller area may observe no selection. We tested for selection of habitat characteristics at several, fine spatial scales,

since we know neither the spatial scale at which dotterel may make choices about their nest sites nor the scale at which factors vary and, to ensure that dotterel were able to make choices at the scales tested, we confined our samples to variable characters.

## METHODS

Dotterel are vulnerable to illegal egg collectors so site names are not given. The data on nest sites were collected from 33 nests on site B from 1996 to 1998 and from 30 nests on site D in 1997 and 1998 (site codes follow Galbraith et al. 1993). Both low-alpine (Horsfield & Thompson 1996) sites were in the Central Highlands of Scotland and were separated by c.8km. The sites were at similar altitudes and shared similar underlying geology.

Data were analyzed using SPSS (Norusis 1990). Two-tailed probabilities are given. We state where data were transformed to normalize their distributions and/or their residuals' distributions.

## HABITAT VARIABLES

We recorded habitat variables at several spatial scales: at the nest, at ten random points within 1m of the nest, at ten random points within 5m of the nest and at ten random points within 25m of the nest. The variables recorded were plant community (*Racomitrium lanuginosum* heath, *Empetrum nigrum/Vaccinium* spp. heath, *Carex bigelowii* snow-bed community, *Nardus stricta* snow-bed community, dwarf *Calluna vulgaris* heath or montane bog), slope of ground (scored as flat, gentle, medium, steep or very steep, corresponding to mean slopes of 1.3, 4.0, 6.4, 9.0 and 13.4°, respectively, measured by the method described for the visibility model), the aspect of the slope, topographic position (scored as top of hill, side of hill or between hills), percentage bare ground within 1m radius (including gravel and small stones, estimated to nearest 5%), percentage bare ground within 5m radius, percentage cover of graminoid tussocks (of *Nardus stricta*, *Eriophorum* spp. and/or *Scirpus cespitosus*, which can all form distinct, relatively tall, dense stands) within 1m and 5m radii, percentage boulders (stones with any above ground dimension more than 15cm) within 1m

and 5m radii, surface roughness (scored 1, 2, or 3; 1=smooth, no hummocks or hags > 15 cm high, 3=more than half of the ground broken by hummocks/hags of a height of at least 30cm, 2=intermediate to scores 1 and 3) within 1m and 5m radii, the distance to the nearest stone with at least one dimension of 10cm (maximum recorded distance of 1m), whether on or by a hummock or hag (defined as within 13cm of a hummock at least 7cm high) and, if so, the direction to the hummock and in what position on the hummock (top, side, bottom, and, if at the bottom, whether at the base on one hummock or between more than one), the height of the hummock and, if between hummocks, the height of and direction to the second hummock (to the nearest cm). Vegetation depth was measured at all random points by resting a 37.5g disc of 8cm diameter on the vegetation surface. The depth of vegetation overlying soil, stone or gravel was then measured using Camlab (Cambridge, UK) calipers' spike at four equally spaced points around the disc's edge. As the disc was smaller in size than some nests, the vegetation depth at nests was measured from the disc resting in four positions where its edge intersected with the edge of the nest, giving four equally spaced points around the nest rim. To test whether measuring method affected measured vegetation depth, we measured vegetation depth at random points by both the nest and non-nest methods. Measuring method had no significant effect on measured vegetation depth and differences between random points accounted for 95% of the variation (general linear model: measuring method  $F_{1,13}=0.853$ ,  $P=0.373$ , random point identity  $F_{6,13}=43.6$ ,  $P<0.001$ ).

#### VISIBILITY FROM THE NEST

An index of the potential visibility of ground predators to an incubating dotterel (ground predator visibility index) was recorded for all nests and at a random point within 50m of each nest. In addition to measuring the visibility from the nest and random point, if sited on a hummock for nests or on or near a hummock for random points, we also measured the visibility from other positions on the hummock (top, side, and bottom and 'no hummock' which was a point 15cm in random direction from the hummock and not on or beside another hummock). 1m tall canes, each marked into five 20cm colored bands, were placed at 25m, 50m, 75m and 100m from the nest on bearings to the north, east, south and west. The percentage of each stick that could be seen through binoculars with one eye 5cm above the

nest cup (i.e. approximately a sitting dotterel's viewpoint) was recorded to the nearest ten percent. The ground predator visibility index score was the summed percentage of canes visible at the 16 positions. An index of the visibility of aerial predators was recorded for 27 nests (six nests were not refound for this work) on site B in 1996-1998 and 30 nests on site D in 1997 and 1998. The aerial predator visibility index was measured by recording, from 5cm above the nest, the angles (using an angle setter) and distances (using a 1:25,000 Ordnance Survey map) to horizons within 500m of the nest, to the north, east, south and west. Avian predators usually flew within 100m of the ground (69% of 55 sightings of corvids and gulls on site B 1996-1998 and site D 1997-1998). For each nest, we recorded the shape of the vertical section of sky within 100m of the ground and 500m of the nest, on each of the four bearings, by measuring the distance between the contour lines on enlarged 1:25,000 Ordnance Survey maps. By plotting the shapes of these sections of sky and the angles visible from the nest together on a grid, we were able to measure the proportion of the sky visible from the nest. The aerial predator visibility index was calculated as the mean percentage of the sections of sky visible from the nest on the four bearings. The aerial predator visibility index was significantly, positively correlated with the visibility of ground predators on both sites (Spearman's rank correlation: site D  $r_s=0.536$ ,  $n=30$ ,  $P=0.002$ , site B  $r_s=0.427$ ,  $n=27$ ,  $P=0.026$ ). The slope of the ground was calculated as the mean absolute slope measured with an angle setter from the top of a 1m cane at the nest or random point to the top of a 1m cane 25m to the north, east, south and west. The shape of the ground was scored for the ground 100m to the north, east, south and west of the nest or random point (1= convex, 2=uncurved, 3= concave). The shape index was the sum of the scores for the four compass bearings.

To allow us to estimate visibility at random points around nests, we derived models (using GLM on square root transformed ground predator visibility index scores) of the effects of habitat variables on the visibility of ground predators recorded at nests and the random points by nests. Visibility significantly differed between hummock positions at both nest and random points (Friedman test: nest  $\chi^2_2=88.64$ ,  $n=55$ ,  $P<0.001$ , random point  $\chi^2_3=53.71$ ,  $n=32$ ,  $P<0.001$ ). To avoid pseudoreplication, we derived separate models for each hummock position (pooling data from nests and random points). We included in the maximal models

those habitat variables that we thought likely to affect visibility. Plant community and shape index were retained in all minimal models, slope in models for top, side and no hummock position, surface roughness within 1m radius and percentage tussocks within 5m radius in the top, side and bottom of hummock models and the percentage tussocks within 1m radius was included in the bottom of hummock model. The surface roughness score for a 5m radius and hummock height were not retained in any minimal models. The models explained 62% of variance in the ground-predator visibility index ( $F=167.2_{1,104}$ ,  $P<0.001$ , only one hummock position used per random point or nest to avoid pseudoreplication).

### HABITAT HETEROGENEITY

Dotterel often site their nests next to stones (Nethersole-Thompson 1973). Stones were not abundant on site B, but bare ground, tussocks and hummocks may also increase heterogeneity, disrupting the outline of the sitting dotterel or exposed eggs. An index of heterogeneity was calculated for each point by summing scores for each of the habitat variables that might increase visual habitat heterogeneity (sum of: one if a stone within 1m, zero otherwise; one if on or by a hummock, zero otherwise; one if at least five percent bare ground, zero otherwise; one if at least five percent tussocks, zero otherwise; one if at least five percent boulders, zero otherwise).

### WIND EXPOSURE

To allow us to estimate the mean wind speed at nests and at the random points around them we developed a model of how wind speed varied with habitat variables. We measured wind speed (to  $0.1\text{ms}^{-1}$ ), using a Kestrel hand-held anemometer (Nielson-Kellerman, Chester, USA) at 160 random points over five days in 1998 on site B. Wind speed was recorded (to  $1\text{ms}^{-1}$ ), simultaneously with 89% of the random point recordings, every 15s, by a Davis Instruments cup anemometer and a LogIt datalogger, at 1.45m above ground at a fixed, open hilltop location on the same site. At each random point we recorded the mean wind speed over 30s at 1.45m above ground. We then recorded wind speed at 0.02m above ground level at all hummock positions (if there was a hummock within 1m of the random point, hummock positions recorded: top, windward side, windward bottom, leeward side, leeward bottom, side-

on to wind side, side-on to wind bottom, neither on nor by hummock). Wind speed was recorded as the mean over 30s, twice at each position. The mean wind speed over 30s at 1.45m above the ground was then recorded again. The mean for the two values for each position was used in analyses. At each random point we also recorded the time period over which the wind speed readings were taken, slope aspect, wind direction, plant community, slope (flat, gentle, medium, steep or very steep), percentage cover tussocks within 1m and 5m radii, percentage cover boulders within 1m and 5m radii and percentage cover bare ground within 1m and 5m radii.

We derived models in two stages to describe the relationship between local wind speed and habitat variables. The first model (using GLM with a square root transformed dependent) described the relationship between habitat variables and wind speed at 1.45m above ground level at sampling points, as a proportion of that simultaneously measured at 1.45m at the weather station. All the habitat variables recorded at points were entered into the maximal model. In all the GLMs presented here, since many associated independent variables were entered into the maximal model, variables were initially retained in subsequent models with  $\alpha$  at 0.1, although  $\alpha$  was 0.05 in minimal models. The minimal model explained 44% of the variance in wind speed at 1.45m at sampling points as a proportion of that at the weather station ( $F_{1,129}=8.357$ ,  $P<0.0001$ ) and included plant community, topographic position, slope and the aspect difference (the difference in degrees between the aspect of the slope and the current wind direction, non-significant but retained as a main effect for the significant interaction term) and an interaction term between aspect difference and slope category. For the second stage in modeling wind speed we derived a set of models (using GLM) for the effects of habitat variables on wind speed at 0.02m above ground level as a proportion of that at 1.45m. We entered into the maximal models all of the habitat variables likely to influence wind exposure at this fine scale (plant community, percentage tussocks within 1m and 5m radii, surface roughness score within 1m and 5m radii and hummock height). Wind speed varied significantly, within sampling points, with hummock position (Friedman test:  $\chi^2_7=129.6$ ,  $n=46$ ,  $P<0.001$ ). To utilize the data for all hummock positions from each sampling point without pseudoreplication, we derived a separate model for each hummock position. We



reclassified data from points that were at the bottom of both the windward side of the 'focal' hummock and a second hummock, as being on the leeward side of the second hummock. The models were based on sample sizes between 60 and 156 points and described between 32% and 49% of variance. The models included plant community (included in models for all positions), percentage tussocks within 1m radius (top of hummocks), percentage tussocks within 5m radius (side of windward side and side of hummock side at right angle to wind direction), hummock height (bottom and side of leeward side of hummock) and whether at the bottom of one or between two hummocks (bottom of leeward side and bottom of side of hummock at right angle to wind). We combined the model of wind speed at 1.45m at sampling points as a proportion of that at the weather station and the set of models of wind speed at 0.02m as a proportion of that at 1.45m at the sampling point, to give estimates of wind speed at 0.02m above ground as a proportion of that measured at the weather station. The estimates from the combined models explained 58% of variance in wind speed at 0.02m as a proportion of that at 1.45m at the weather station ( $F=192.0_{1,138}$ ,  $P<0.001$ , only one hummock position included per sampling point to avoid pseudoreplication).

Wind directions differ in frequency and mean speed varies between wind directions. To estimate wind exposure at points on sloping ground and on the side or bottoms of hummocks (i.e. where exposure depended on the wind direction), we weighted the wind exposure estimates by the frequencies and speeds of winds from different directions. Our weather stations did not record wind direction so we used wind speed and direction data collected by Heriot-Watt University's automatic weather station (AWS) on the summit of Cairn Gorm, approximately 40km from sites B and D. We confined wind data to the six years between 1990 and 1999, inclusive, when there were Cairn Gorm wind speed data for at least 60% of the range of Julian dates that included 95% of the sample dates on which dotterel incubated, extrapolating from first egg dates. The Cairn Gorm weather station was taller and at higher altitude than the weather station on site B so would be expected to record higher wind speeds (HMSO 1982; McClatchey 1996). Simultaneous wind speed records on sites B and Cairn Gorm were significantly, positively associated ( $F_{1,5909}=4155.87$ ,  $P<0.001$ ,  $R^2_{adj}=0.413$ ) and wind speed on site B was a mean of  $0.582 \pm 0.012$  (95% c.i.) of Cairn Gorm wind speed. Wind

speeds recorded simultaneously by site B weather station and a handheld anemometer 1.45m above ground on site D did not significantly differ ( $t_{18}=1.219$ ,  $P=0.239$ ) so mean wind speeds for different wind directions on both sites B and D were calculated by multiplying Cairn Gorm values by 0.582. Wind exposure estimates for points were calculated for wind blowing from eight directions (north, north-east, east, south-east, south, south-west, west and north-west), weighting the value for each direction by the mean wind speed from that direction and the proportional frequency of wind from that direction. The model for wind speed at 0.02m as a proportion of that at 1.45m included only four wind directions (windward, leeward and side-on on each side of a hummock): we estimated the proportion for the remaining intermediate four points as the mean of those estimated for the adjacent two. The wind exposure value for each point estimates the mean wind speed at 0.02m above ground level under average wind direction and speed conditions.

## NEST DIMENSIONS

The total depth of the nest cup (including the lining), the depth of the lining and the distance from the lining to the top of the nest were measured with the spike of calipers to the nearest mm. Only lining depths measured while nests were active are included in analyses as nesting-failure or hatched chicks may change the distribution of nest lining, affecting lining depth (S. Holt unpublished). The distance from the top of the eggs to the top of the cup was estimated by eye to the nearest 5mm. After nest were vacated, nest linings were collected, air-dried and their volumes measured to the nearest 10ml in a graduated vessel.

## RESULTS

### NEST SITE SELECTION

Dotterel selected nest sites that were significantly more heterogeneous and had significantly deeper vegetation than the surrounding 1m radius area of ground. The vegetation within 1m radius of nests was significantly shallower than within 5m. We found no significant differences in heterogeneity or vegetation depth at any other spatial scales, and no differences in wind exposure and visibility at any scale tested (Table 1). Multiple tests of the same hypothesis or

data set can result in an increased number of Type II errors (Rice 1989). When we applied a sequential Bonferonni adjustment for multiple tests to the 13 tests of habitat selection, all initially significant tests remained significant at  $P < 0.05$ .

Table 1. Nest site selection: To test whether dotterel preferentially selected nest sites in relation to visibility, heterogeneity, wind exposure or vegetation depth we calculated, for each nest, the mean value of each variable for each of the sampling bands (bands of 1m, 5m and 25m radii from the nest). We made pairwise comparisons, using Wilcoxon signed-ranks tests, of the values of each variable at the nest and in the 1m band, in the 1m and 5m bands and in the 5m and 25m bands. Sites B and D were treated as replicates and we give their combined probability for each test. Since dotterel can only show selection for characters that vary, we excluded from analyses any pair in which there was no variation within that distance band.

	spatial scales compared	combined probability $\chi^2_4$	probability $P$	median of smaller-larger scale		$N$		source of data
				site B	site D	site B	site D	
visibility	nest v. 50m	4.59	>0.05	40	20	33	30	measured
	nest v. 1m	6.78	>0.05	-9	-7	28	14	estimated from model
	1m v. 5m	6.81	>0.05	-3	-4	32	26	estimated from model
	5m v. 25m	1.27	>0.05	5	4	33	30	estimated from model
habitat heterogeneity	nest v. 1m	19.21	0.0016	0.3	0.2	31	28	measured
	1m v. 5m	4.96	>0.05	0	0.15	33	30	measured
	5m v. 25m	5.28	>0.05	0.1	0	33	30	measured
wind exposure	nest v. 1m	1.26	>0.05	0.0ms <sup>-1</sup>	-0.1ms <sup>-1</sup>	33	29	estimated from model
	1m v. 5m	1.48	>0.05	0.0ms <sup>-1</sup>	-0.1ms <sup>-1</sup>	33	29	estimated from model
	5m v. 25m	3.72	>0.05	0.1ms <sup>-1</sup>	0.0ms <sup>-1</sup>	33	30	estimated from model
vegetation depth	nest v. 1m	46.53	0.0002	18.4mm	25.8mm	33	30	measured
	1m v. 5m	24.95	0.0002	-6.7mm	-9.3mm	33	30	measured
	5m v. 25m	11.08	>0.05	-1.4mm	-2.5mm	33	30	measured

## VEGETATION DEPTH AND NEST DIMENSIONS

The volume of the nest lining significantly increased with vegetation depth (linear regression: both variables square root transformed,  $\beta$ (back transformed)=0.764,  $F_{1,59}=10.877$ ,  $P=0.002$ ,  $R^2=0.141$ ). The distance from the top of the nest lining to the top of the cup and, consequently, the distance from the tops of the eggs to the top of the cup, increased with vegetation depth (linear regression: lining to top of cup:  $\beta=0.128$ ,  $F_{1,30}=5.351$ ,  $P=0.028$ ,  $R^2=0.123$ ; top of eggs to top of cup, both variables square root transformed,  $\beta$ (back transformed)=0.135,  $F_{1,17}=5.594$ ,  $P=0.030$ ,  $R^2=0.203$ ).

## DISCUSSION

Dotterel breed in cool, wet and windy Arctic-Alpine environments where the energetic costs of thermoregulation and incubation are likely to be high (Piersma & Morrison 1994; Tulp et al. 1998; Andreev 1999) and, since most breeding attempts are uniparental, foraging time to recoup costs is limited (Kálás 1986). To maximize their own and their eggs' survival, dotterel should select nest sites that minimize energy expenditure. Wind exposure is an important determinant of the energetic costs of thermoregulation in shorebirds so, to minimize costs, dotterel should select nest sites sheltered from wind. Using our models and mean recorded wind speeds, a bird nesting on top of a hummock would experience wind speeds a mean of  $1\text{ms}^{-1}$  greater than if it nested at the bottom of the hummock. Using Wiersma & Piersma's (1994) model for the red knot (*Calidris canutus*: another species of shorebird that nests in a cold climate) and their range of coefficients for the effect of wind speed and a mean air temperature of  $8^{\circ}\text{C}$ , the energetic cost of thermoregulation would be between 5% and 21% of the basal metabolic rate (estimated according to Kersten & Piersma 1986) higher on the top of a hummock than at the bottom. In spite of potentially high local variation in energetic costs with nest site location, we found no selection for less windy sites.

Dotterel built their nests in vegetation that was significantly deeper than that within a 1m radius. Nests in deeper vegetation had more nest lining and the eggs sat lower in the cup. Larger nest linings are likely to reduce the rate of heat loss from the eggs to the ground (Collias & Collias 1984) and so reduce the energetic cost of incubation to the parent. A better insulated nest lining may also provide a more favorable thermal environment for embryonic development by reducing the temperature gradient from the hot brood patch to the cool base of the egg. While the parent is absent from the nest, eggs that sit deeper in the cup probably experience lower wind speeds and so have lower cooling rates. This may reduce the energetic cost of egg re-warming when the parent returns to the nest and decrease the time embryos spend below a temperature suitable for development. There is variation between nests in how much of the incubating dotterel's body is inside the nest cup (pers. obs). More of the parent's body may be inside nests when the eggs sit well below the nest rim: the tops of

eggs were from 5mm above the ground level to 25mm below the nest rim (the modal value was level with the ground: nine of 19 nests). This may reduce the rate of passive and forced convective cooling, reducing the energetic cost of thermoregulation (Calder 1973a).

Shorebirds often site their nests near conspicuous objects or on disruptive substrates where they and their exposed eggs may be less likely to be seen by predators (Maclean & Moran 1965; Graul 1975; Nethersole-Thompson & Nethersole-Thompson 1981; Colwell & Oring 1990). Using a composite score of habitat heterogeneity, dotterel selected nest sites that were significantly more visually heterogeneous than the surrounding 1m radius, possibly reducing their own and/or their exposed eggs conspicuousness.

Birds often select nest sites that are well concealed from predators (e.g. Holway 1991; Colwell 1992; Braden 1999). However, if the predator does not have a clear line of sight to a concealed nest, then the nesting bird may be unable to see the predator, so that nest site selection may have to trade-off nest concealment and view of predators (Götmark et al. 1995). Dotterel nest in habitats where short vegetation may not permit effective nest concealment and so they may have to rely principally on their own and their eggs' cryptic coloration and early predator detection to avoid nest predation: in this study we tested whether dotterel selected nest sites with good visibility. There was no evidence, at any spatial scale tested, that dotterel selected nest sites that gave them better visibility of approaching ground predators. As the indices of the visibility of ground and aerial predators were positively correlated, the visibility of ground predators should reasonably summarize the visibility of predators in general.

Fine scale variation in visibility may be relatively unimportant in dwarf vegetation on open alpine plateaux where visibility would be expected to be relatively unobstructed compared with most other habitats. Even so, only a median of a quarter of the cane positions could be seen at all from nests and a median of 70% of the measured airspace was visible. Although incubating dotterel do sometimes respond when avian predators are at a considerable distance from the nest (e.g. flushing to a short-eared owl *Asio flammeus* at c.400m, pers.

obs.), it appears that their fine-scale nest site selection maximises inconspicuousness but not early detection of predators. Byrkjedal & Thompson (1998) suggest that golden plovers, *Pluvialis* spp., nest in short vegetation to maximize their view of predators. Dotterel were able to select deep vegetation without compromising visibility as, within random points within 1m of nests, there was no significant correlation between vegetation depth and estimated visibility (combined probability for Spearman's rank correlation for 61 nests,  $\chi^2_{122}=89.53$ ,  $P=0.988$ ). The plant communities in which dotterel nested in this study generally formed dense mats that provided a substrate within which to build nests, but with relatively little plant matter standing above the mat to impede visibility. *Nardus stricta* snow-bed community, where relatively tall and dense grass blades would stand above the nest cup, was a marked exception to this. This community was avoided as a nest site on site B (Holt & Whitfield 1996b) but on a higher altitude site where *Nardus stricta* was shorter (Whitfield pers. obs.) it was the preferred nest site (Holt & Whitfield 1996a). However other factors, such as an increased need for wind shelter in a harsher, higher altitude environment or the availability of alternative nesting habitat could have caused the difference in nest site selection between the sites.

Nest site selection may trade-off factors such as concealment, visibility of predators, risk of clutch trampling, parental energetic costs, egg chilling, food accessibility and social interactions (Marzluff 1988; Götmark et al. 1995; Ille et al. 1996; Hagelin & Miller 1997). We found no significant selection for either low wind exposure or a good visibility, but the estimated values of wind exposure and visibility were positively correlated (combined probability for Spearman's rank correlation for random points within 1m of 61 nests,  $\chi^2_{122}=906.84$ ,  $P<0.001$ , median  $r_s=0.89$ ), so that an individual selecting good visibility would incur high thermoregulatory costs and vice versa. Perhaps, then, the lack of selection for these characters, at the spatial scales measured, is a consequence of dotterel trading-off these two requirements. Alternatively, the lack of significant selection for either visibility or wind exposure may reflect the incomplete explanation of variation by the two sets of models. Despite our findings, dotterel may have selected nest sites with low wind exposure and/or good visibility in relation to habitat features excluded from, or poorly parameterized in the models. The model of visibility explained 62% of variation in the data-set from which it was

derived, and the model for wind exposure 58%: both will probably explain less variation when applied to different samples of points. However, much of the unexplained variation in the models is likely to be measurement error that cannot be attributed to any factor excluded from or poorly estimated by the models. For example, the weather station anemometer had a resolution of only  $1\text{ms}^{-1}$  (although using the mean for a median of 22 wind speed records per point improved this resolution), whereas the hand-held anemometer recorded to  $0.1\text{ms}^{-1}$ . Additionally, the short time scale over which wind speed varies would also have introduced measurement error, when comparing local means to weather station means measured over a longer period. Since unbiased measurement error probably accounts for much of the unexplained variance in the models, they probably estimate reasonable and unbiased indices of wind exposure and visibility and hence it is unlikely that dotterel selected sites of low exposure or a good visibility at the spatial scales measured.

This study highlights some of the major problems of studies of habitat selection. Observed habitat preferences can vary with the spatial scale investigated (Pribil & Picman 1997). In this study dotterel selected nest sites where the vegetation was significantly deeper than that within 1m of the nest, but where the vegetation within 1m of the nest was significantly shallower than that within 5m of the nest. Likewise, although we found no evidence for selection with respect to wind exposure at fine scales, the mean estimates of wind exposure within 25m of nests were significantly higher than those within the entire study areas, on both sites (Holt unpublished). Many descriptive studies of habitat selection attempt to determine important habitat characteristics with no *a priori* reasons for predicting at what spatial scale selection will occur. However, to test *a priori* hypotheses, it is important to choose spatial scales at which there is sufficient variation to allow choice and to confer fitness benefits on individuals that make certain selections. We know that visibility, wind exposure, vegetation depth and visual habitat heterogeneity all vary at a fine spatial scale, and that the first three parameters show much variation even over the same hummock. An area of ground only as large as a nest could confer benefits if it was either sheltered, gave good visibility or had deep vegetation. Although we do not know how large an area of visually heterogeneous habitat is required to decrease nest conspicuousness, it seems likely that the patches of nearly 0.2ha,

enclosed within the 25m radius should, at least, be large enough to decrease conspicuousness. Dotterel can, then, potentially make choices for vegetation depth, visibility, wind exposure and, probably, visual heterogeneity at the spatial scales tested. We have insufficient statistical power, in this study, to test whether these levels of variation will have consequences for reproductive value. Even in more powerful data sets, variation in habitat variables may have no effect on hatching success if individuals are able to compensate for poor nest sites (Cresswell 1997). Individuals may, for example, be able to use stored energy reserves or reduce nest attendance to compensate for higher energetic costs, or increase vigilance to accommodate an increased risk of detection by predators.

A principal problem in interpreting the results of studies of habitat selection is association between habitat variables. For example, although dotterel's nesting areas were windier than the study areas as a whole, this was unlikely to be a consequence of selection for a windy position *per se*, but rather of selection for some other associated habitat characteristic, such as proximity to dotterel's preferred plant communities for feeding, which tend to occur in higher, more exposed locations (Galbraith et al. 1993; Brown et al. 1993). In this study, we attempted to avoid the potentially confounding effects of other associated habitat selection criteria, such as proximity to preferred feeding areas, by investigating only very fine spatial scales at which only a small number of habitat characteristics were likely to be important.

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## REFERENCES

- Andreev,A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich , 70, 13-22.
- Austin,G.T. 1974. Nesting success in the Cactus Wren in relation to nest orientation. The Condor , 76, 216-217.
- Austin,G.T. 1976. Behavioural adaptations of the Verdin (*Auriparus flaviceps*) to the desert environment. Auk , 93, 245-262.
- Braden,G.T. 1999. Does nest placement affect the fate or productivity of California Gnatcatcher nests? Auk , 116, 984-993.
- Brown,A., Horsfield,D. & Thompson,D.B.A. 1993. A new biogeographical classification of the Scottish uplands .1. Descriptions of vegetation blocks and their spatial variation. Journal of Ecology , 81, 207-230.
- Buitron,D. 1983. Variability in the responses of Black-billed Magpies to natural predators. Behaviour , 87, 209-236.
- Byrkjedal,I. 1987. Antipredator behaviour and breeding success in Greater Golden Plover and Eurasian Dotterel. The Condor , 89, 40-47.
- Byrkjedal,I. & Thompson,D.B.A. 1998. Tundra Plovers: The Eurasian, Pacific and American Golden Plovers and Grey Plover. London: T&AD Poyser.
- Calder,W.A. 1973a. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comparative Biochemistry and Physiology , 46, 291-300.
- Calder,W.A. 1973b. Microhabitat selection during nesting in hummingbirds in the Rocky Mountains. Ecology , 54, 127-134.
- Collias,N.E. & Collias,E.C. 1984. Nest building and bird behaviour. Cambridge: Harvard University Press.
- Colwell,M.A. 1992. Wilson's Phalarope nest success is not influenced by vegetation concealment. The Condor , 94, 767-772.
- Colwell,M.A. & Oring,L.W. 1990. Nest-site characteristics of prairie shorebirds. Canadian Journal of Zoology , 68, 297-302.

- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic: Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Cresswell, W. 1997. Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. Animal Behaviour, 53, 93-103.
- Ford, H.A. 1999. Nest site selection and breeding success in large Australian Honeyeaters: Are there benefits from being different? Emu, 99, 91-99.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D.P. & Thompson, D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. Ibis, 135, 148-155.
- Gloutney, M.L. & Clark, R.G. 1997. Nest-site selection by Mallards and Blue-winged Teal in relation to microclimate. Auk, 114, 381-395.
- Götmark, F., Blomqvist, D., Johansson, O.C. & Bergkvist, J. 1995. Nest-site selection - a trade-off between concealment and view of the surroundings. Journal of Avian Biology, 26, 305-312.
- Graul, W.D. 1975. Breeding biology of the Mountain Plover. Wilson Bulletin, 87, 6-31.
- Hagelin, J.C. & Miller, G.D. 1997. Nest-site selection in South Polar Skuas: Balancing nest safety and access to resources. Auk, 114, 638-645.
- Halupka, K. 1998. Nest-site selection and nest predation in meadow pipits. Folia Zoologica, 47, 29-37.
- HMSO 1982. Observer's Handbook. 4th edn. London: HMSO.
- Holt, S. & Whitfield, D.P. 1996a. Montane Ecology Project report series: [study area A].  
Edinburgh: Scottish Natural Heritage
- Holt, S. & Whitfield, D.P. 1996b. Montane Ecology Project site report series: [study area B].  
Edinburgh: Scottish Natural Heritage
- Holt, S. & Whitfield, D.P. 1996c. Montane Ecology Project site report series: [study area C].  
Edinburgh: Scottish Natural Heritage
- Holt, S., Whitfield, D.P., Duncan, K., Rae, S. & Smith, R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? Journal of Avian Biology, 33, 219-224
- Holway, D.A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. The Condor, 93, 575-581.

- Hooge, P.N., Stanback, M.T. & Koenig, W.D. 1999. Nest-site selection in the Acorn Woodpecker. Auk , 116, 45-54.
- Horsfield, D. & Thompson, D.B. 1996. The uplands: guidance on terminology regarding altitudinal zonation and related terms. Information and Advisory Note 26. Battleby, UK: SNH
- Ille, R., Hoi, H. & Kleindorfer, S. 1996. Brood predation, habitat characteristics and nesting decisions in *Acrocephalus scirpaceus* and *A. palustris*. Biologia , 51, 219-225.
- Joern, W.T. & Jackson, J.F. 1983. Homogeneity of vegetational cover around the nest and avoidance of nest predation in Mockingbirds. Auk , 100, 497-499.
- Kálás, J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Kálás, J.A. & Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). Auk , 101, 838-847.
- Kersten, M. & Piersma, T. 1986. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea , 75, 175-188.
- Koivula, K. & Ronka, A. 1998. Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's Stint (*Calidris temminckii*). Oecologia , 116, 348-355.
- Maclean, G.L. & Moran, V.C. 1965. The choice of nest site in the White-fronted Sandplover *Charadrius marginatus* Vieillot. Ostrich , 36, 63-72.
- Martin, T.E. 1988. Nest placement: implications for selected life-history traits, with special reference to clutch size. American Naturalist , 132, 900-910.
- Martin, T.E. & Roper, J.J. 1988. Nest predation and nest-site selection of a western population of hermit thrush. The Condor , 90, 51-57.
- Marzluff, J.M. 1988. Do Pinyon Jays alter nest placement based on prior experience. Animal Behaviour , 36, 1-10.
- McClatchey, J. 1996. Spatial and altitudinal gradients of climate in the Cairngorms-observations from climatological and automatic weather stations. Botanical Journal of Scotland , 48, 31-49.

- Møller,A.P. 1987. Egg predation as a selective factor for nest design: an experiment. Oikos , 50, 91-94.
- Møller,A.P. 1989. Nest predation selects for small nest size in the blackbird. Oikos , 57, 237-240.
- Nelson,K.J. & Martin,K. 1999. Thermal aspects of nest-site location for Vesper Sparrows and Horned Larks in British Columbia. Studies in Avian Biology , 19, 137-143.
- Nethersole-Thompson,D. 1973. The Dotterel. Glasgow: Collins.
- Nethersole-Thompson,D. & Nethersole-Thompson,C. 1981. Greenshanks. Berkhamsted: T & AD Poyser.
- Nias,R.C. 1986. Nest-site characteristics and reproductive success in the Superb Fairy-Wren. Emu , 86, 139-144.
- Norusis,M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Gorinchem: SPSS Ltd.
- Orians,G.H. & Wittenberger,J.F. 1991. Spatial and temporal scales in habitat selection. American Naturalist , 137, S29-S49
- Osborne,P. & Osborne,L. 1980. The contribution of nest characteristics to breeding success among blackbirds *Turdus merula*. Ibis , 122, 512-517.
- Petersen,M.R. 1990. Nest-site selection by Emperor Geese and Cackling Canada Geese. Wilson Bulletin , 102, 413-426.
- Piersma,T. & Morrison,R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.
- Pribil,S. & Picman,J. 1997. The importance of using the proper methodology and spatial scale in the study of habitat selection by birds. Canadian Journal of Zoology , 75, 1835-1844.
- Pulliainen,E. & Saari,L. 1992a. Body mass and physical condition of breeding Dotterels *Charadrius morinellus* in Finland. Oecologia Montana , 1, 1-4.
- Pulliainen,E. & Saari,L. 1992b. Breeding biology of the Dotterel, *Charadrius morinellus*, in eastern Finnish Lapland. Ornis Fennica , 69, 101-107.
- Pulliainen,E. & Saari,L. 1995. Inter- and intraspecific reactions of incubating Dotterel *Charadrius morinellus* in Finland. Wader Study Group Bulletin , 78, 36-38.

- Rands, M.R.W. 1988. The effect of nest site selection on nest predation in Grey Partridge *Perdix perdix* and Red-legged Partridge *Alectoris rufa*. Ornis Scandinavica , 19, 35-40.
- Regehr, H.M., Rodway, M.S. & Montevecchi, W.A. 1998. Antipredator benefits of nest-site selection in Black-legged Kittiwakes. Canadian Journal of Zoology , 76, 910-915.
- Rice, W.R. 1989. Analysing tables of statistical tests. Evolution , 43, 223-225.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smiths. Cont. Zool. 9, 1-48.
- Seitz, L.C. & Zegers, D.A. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. The Condor , 95, 297-304.
- Sockman, K.W. 1997. Variation in life-history traits and nest-site selection affects risk of nest predation in the California Gnatcatcher. Auk , 114, 324-332.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Annales Zoologici Fennici , 4, 158-198.
- Stokes, D.L. & Boersma, P.D. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). Auk , 115, 34-49.
- Tarvin, K.A. & Smith, K.G. 1995. Microhabitat factors influencing predation and success of suburban Blue Jay *Cyanocitta cristata* nests. Journal of Avian Biology , 26, 296-304.
- Tulp, H., Schekkerman, H., Piersma, T., Jukema, J., de Goeij, P., & van de Kam, J. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. 61. Zeist, The Netherlands: WIWO
- Tuomenpuro, J. 1991. Effect of nest site on nest survival in the Dunnock *Prunella modularis*. Ornis Fennica , 68, 49-56.
- Wachob, D.G. 1996. A microclimate analysis of nest-site selection by Mountain Chickadees. Journal of Field Ornithology , 67, 525-533.
- Wiersma, P. & Piersma, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Wilkie, A.O.M. 1980. Incubation Behaviour of the Dotterel. In: Cambridge Norwegian Expedition 1978 Report (Ed. by J.L.Innes), pp. 34-58. Cambridge: Cambridge University.
- With, K.A. & Webb, D.R. 1993. Microclimate of ground nest: the relative importance of radiative cover and wind breaks for three grassland species. The Condor , 95, 401-413.

Zerba,E. & Morton,M.L. 1983. Dynamics of Incubation in Mountain White-crowned Sparrows.

The Condor , 85, 1-11.

## Chapter 7

### ENERGETIC CONSTRAINT AND REPRODUCTIVE TRADE-OFFS IN NEST DEFENCE BY EURASIAN DOTTEREL

S. HOLT\*, D.P. WHITFIELD\*\*, R. DENNY\*\*, I. DILLON\*\*, K. DUNCAN\*\*, J. GORDON\*\*, A.  
MEE\*\*\*, D. PULLAN\*\*, S. RAE\*\*, R.D. SMITH\*\*, J. STIRLING\*\*

\*Institute of Biological Sciences, University of Stirling

\*\*Scottish Natural Heritage, Edinburgh

\*\*\*Department of Animal and Plant Sciences, Sheffield University

#### ABSTRACT

Many studies that investigate variation in parental investment use the intensity of nest defence as a measure of parental investment and assume that more intense responses decrease the probability of offspring predation. However, in this study of Eurasian dotterel *Charadrius morinellus* there was no clear relationship between the 'intensity' of the defensive response to humans and the probability of clutch predation. Correspondingly, dotterels' responses to human simulated predators did not vary with two predictions from life history theory based on the reproductive values of the parent and offspring: flushing distance did not vary with stage of breeding or parent age. Instead, responses varied according to changing egg-exposure costs and, probably, with an individual's ability to bear those costs. In poorer weather and when nesting at higher altitude, dotterel flushed from the nest when a human was closer. We interpret this to be a consequence of the higher energetic cost of periods of egg exposure in colder conditions as dotterel tended to flush at longer distances during a period of increased food abundance, when their energetic expenditure would have been less constrained. Dotterel did not vary their responses according to our measures of their experience of people. Approximately half the variation in flushing distance was explained by differences between individuals.

## **INTRODUCTION**

Nest predation is the principal cause of reproductive failure many bird species (Ricklefs 1969). The way in which a parent responds to a potential predator approaching its nest can influence whether the nest is depredated (Wiklund 1990a; Sjoberg 1994; review in Hatch 1997), so the effectiveness of nest defence behaviour may be a major determinant of lifetime reproductive success. When nest defence carries costs for the parent, it is a component of parental investment (Andersson et al. 1980; Rytönen et al. 1995; King 1999). Predictions about parental investment in nest defence can be made from life history theory, based on the reproductive values of the parent and offspring (Montgomerie & Weatherhead 1988). In keeping with prediction from life history theory, many studies have found that, as a breeding attempt progresses and the probability of survival and hence reproductive value of the offspring increases, the intensity of nest defence increases (Larson 1960; Gramza 1967; Barash 1975; Andersson et al. 1980; Greig-Smith 1980; Patterson et al. 1980; East 1981; Regelman & Curio 1983; Reid & Montgomerie 1985; Westmoreland 1989; Westneat 1989; Rytönen et al. 1990; Wiklund 1990b; Amat et al. 1996) (although in some studies this may be a consequence of habituation to the simulated predator, Knight & Temple 1986). Similarly, seasonally breeding species should increase investment in nest defence through the season if the probability of initiating a successful replacement clutch declines (Montgomerie & Weatherhead 1988). Another prediction from life history theory is that older parents should invest more in nest defence if their own residual reproductive value declines with age (Wallin 1987; Montgomerie & Weatherhead 1988; Sjoberg 1994).

The most frequently considered cost of nest defence is the risk to the parent through close proximity to an egg-predator that may also be dangerous to the parent (Myers 1978; Andersson et al. 1980; Reid & Montgomerie 1985; Dale et al. 1996; King 1999). However, there may be other costs: nest defence may be costly in terms of energy or time (Ueta 1999; Komdeur & Kats 1999), cause the parent physiological stress (Graul 1975; Regelman & Curio 1983) or, if the parent leaves the nest, the offspring may become chilled or overheated (Dale et al. 1996).



The Eurasian dotterel *Charadrius morinellus* is a shorebird (Charadrii) that nests on the ground in the cool arctic-alpine zone of the Palaearctic (Cramp & Simmons 1983). Incubating dotterel exhibit a variety of nest defence responses to a human approaching the nest: birds may flee while a human is over a hundred metres from the nest or may only flush from the nest when touched and then perform a 'distraction display' very close to the human (Cramp & Simmons 1983). Distraction displays involve apparent attempts to lead the human from the nest with injury feigning, vocalisations, 'rodent-running' and 'false brooding' (Cramp & Simmons 1983). The range of dotterels' reactions to humans approaching the nest appears similar to their range of reactions to approaching predators, although dotterel do not tail-flag to humans as they sometimes do to avian predators and some dotterel allow themselves to be touched by humans or, very rarely, 'explode' at humans as at non-predatory ungulates (pers. obs.; Nethersole-Thompson 1973; Wilkie 1980; Cramp & Simmons 1983).

Interacting with a predator during active nest defence probably places a dotterel at a greater risk of capture by the predator but leaving the nest in response to an approaching predator will cause the eggs to cool rapidly in an arctic-alpine environment. The degree of cooling will vary with weather conditions and the length of exposure. Egg cooling carries two potential costs for an incubating dotterel. First, the development of embryos will pause below the physiological zero temperature and there may be lethal or sub-lethal effects of prolonged exposure to low temperatures (Webb 1987). Second, when the parent returns to the nest after nest defence, it must re-warm the cooled eggs. Breeding arctic-alpine shorebirds can have high energetic costs (Kersten & Piersma 1986; Piersma & Morrison 1994) that, in the case of the dotterel, are usually born by a single individual with restricted foraging time in which to recoup costs (Kálás 1986). Dotterel should, therefore, be particularly sensitive to the energetic costs of nest defence, such as expensive egg re-warming.

The variation in the nest defence behaviour of incubating dotterel and their probable sensitivity to a range of potential costs of nest defence makes the species a good subject for testing the roles of life history and energetic costs in shaping nest defence behaviour. In this study, we test if nest defence behaviour varies according to life history theory predictions

based on the trade-off between the parent and offspring's reproductive value. Specifically, we test whether dotterel's investment in nest defence increases with the stage of breeding, through the season and with the parent's age. We also investigate whether the varying egg-exposure costs of different responses affect nest defence behaviour. Egg cooling rates will depend on the current weather conditions (Chapter 3) and average weather conditions will deteriorate with increasing altitude (local lapse rates predict that the dotterel at the highest nest in the sample experienced temperatures very roughly 3.8°C lower and wind speeds 3.5ms<sup>-1</sup> higher than the lowest bird, McClatchey 1996). We test the prediction that the nest defence behaviour of dotterel varied in order to reduce egg-exposure in colder conditions (i.e. during poor weather and at higher altitudes). Egg chilling may affect embryonic development and/or the energetic egg re-warming costs to the parent. If the cost to the parent of re-warming eggs is important in determining a nest defence response then responses should vary between periods of higher and lower food abundance. We test whether more energetically costly nest defence responses were made in periods of higher food abundance when energy expenditure should be less constrained.

Prior experience of humans or habituation to a simulated egg-predator can be a source of variation in nest defence and, because we used humans as simulated predators, could confound our analyses (Knight & Temple 1986). The abundance of people varied greatly between study areas (from less than five to over one hundred people visiting a study area per day, Amphlett 1995; Holt & Whitfield 1996a; Holt & Whitfield 1996b; Holt & Whitfield 1996c; A. MacColl et al. unpublished data) so we tested whether nest defence varied according to the abundance of people in a study area. As most human visitors stayed on a path (Amphlett 1995; Holt & Whitfield 1996a; A. MacColl et al. unpublished data) a dotterel's experience of people will also have varied with the distance of the nest from a path, so we tested whether nest defence responses varied with the distance of the nest from a path.

## **METHODS**

We collected data on nest defence responses during 1990-1998 from 382 dotterel nests on eight low and mid-alpine (Horsfield & Thompson 1996) study sites in the Central Highlands of Scotland. Dotterel are vulnerable to egg collectors so the study sites are not named. All observers were licensed to disturb nesting dotterel and we only collected data opportunistically, when visiting nests to monitor breeding success. To estimate clutch predation rates, nests were regularly checked and clutches were classed as depredated when they disappeared before the expected hatch date and/or when shell remains with beak or tooth marks or predator faeces, urine or feathers were found in or by the nest. The date that a clutch was initiated (first egg date) was observed, estimated from hatch date (assuming a 28 day period from first egg laid to last chick hatched, Cramp & Simmons 1983; D.P. Whitfield unpublished data) or estimated from an equation relating egg density to days until hatch (derived from measurements of clutches of known hatch date, D.P. Whitfield unpublished data). Nest altitude and the distances of nests to the nearest path were recorded to the nearest 10m from plots of nest locations on large scale Ordnance Survey maps.

We approached incubating dotterel directly, at normal walking speed. We recorded the distance between the observer and the nest at which the dotterel left the nest (subsequently referred to as flushing distance), the type of response made on flushing (response type), the maximum distance the dotterel moved away from the observer at the nest (distance flushed to) and the minimum distance to which the dotterel approached the observer when the observer was at the nest (approach distance). Response types were categorised as 'interaction' responses (distraction displays and/or when the bird ran or flew off the nest towards the approaching observer) or 'fleeing' responses (when the bird ran or flew off the nest away from the observer with no distraction display).

We recorded a mean of 2.4 nest defence records per nest and we state when we use the nest-means of flushing distance in analyses. Dotterel at 69% of nests were individually recognisable by colour-rings or, for one individual, by an abnormal wing. To minimise

pseudoreplication we included only one datum (randomly selected unless otherwise stated) per recognisable individual in analyses, other than when investigating variation between individuals or egg-predation rates.

Dotterel were sexed in the field using plumage characters and trapped birds were aged in the hand as first summer birds or as birds in at least their second summer using the degree of outer primary wear and the retention of juvenile inner median coverts (Whitfield 1999). For birds that had been colour-ringed in a previous year, ringing records were used to place a bird at an exact age (if initially captured as a first summer bird or pullus) or at a minimum age (if older when first captured). We excluded females from the analyses since most nests were incubated by the male alone and, at biparental nests, there was a non-significant tendency for the female to flush at a shorter distance than their mate (paired *t*-test:  $t_{14}=1.92, P=0.076$ , flushing distance of a female was a mean of 10.7m less than that of her mate).

We could test for the effects of weather conditions only on site A (1990-93) and sites B and D (1997-98), where there were weather stations. Weather records for site A were from Heriot-Watt University's Automatic Weather Station (AWS), using shaded air temperature and wind speed (the mean over 2.5 minutes) from the half-hourly record that was closest in time to nest defence records in analyses. The AWS recorded weather variables at 4m above ground level at an exposed location. Wind speed for sites B and D (8km apart) was recorded at 1.45m above ground level at 1.35 minute intervals by an automatic weather station on site B. The mean of the three consecutive instantaneous wind speed records, closest in time to the recorded nest defence response, was used in analyses. Wind speeds were standardised to estimated values at 10m above ground level using the equation in HMSO (1982). Shaded air temperature was recorded at 1.2m above ground at between 1.35 and 3.2 minute intervals by automatic weather stations on sites B and D, and the record that was closest in time to a nest defence response was used in analyses. As air temperature was measured at different heights above ground level on site A and sites B and D, the temperature difference used in analyses may not have corresponded to the same temperature differences experienced by dotterel at ground level (Geiger et al. 1995).

We recorded all people we saw while on the study sites. We calculated an index of the abundance of people on each site as the number seen per day from May to August inclusive, combining days from all years. We combined years as numbers of people on sites appeared consistent across years (A. MacColl at al. unpublished data) and pooling years probably improved estimates for site-years when few visits were made.

Adults of the crane fly species *Tipula montana* are relatively large and slow moving and, during the emergence period, very abundant. When available, they formed an important part of dotterel's diet (Galbraith et al. 1993). We measured the abundance of adult *T. montana* from transects. Approximately every three days, the observer slowly walked between five and ten 10m transects and counted the number of adult *T. montana* seen in a 2m band centred along each transect.

Statistical tests were carried out using SPSS (Norusis 1990). Two-tailed probabilities are given. We state where data were transformed to normalise their distributions and/or their residuals' distributions. Non-parametric tests were used where data could not be readily transformed to approximate a normal distribution.

## **RESULTS**

### **The Nest Defence Response**

Interaction responses were made at significantly shorter flushing distances than fleeing responses (*t*-test:  $t_{273}=9.39$ ,  $P<0.001$ , Interaction mean=3.3m, fleeing mean=15.6m, Fig. 1). To ensure that this result was not simply a consequence of observers' reduced ability to see interaction responses at longer flushing distances, we repeated the test, confining flushing distances to less than 20m. In this subset of the data, interaction responses were still made at significantly shorter flushing distances than fleeing responses (*t*-test:  $t_{211}=3.30$ ,  $P=0.001$ ).

Distance flushed to and approach distance were both positively correlated with flushing distance (Spearman rank correlation:  $r_s=0.73$ ,  $N=268$ ,  $P<0.001$ ;  $r_s=0.67$ ,  $N=251$ ,  $P<0.001$ , respectively). The amount of time observers spent at the nest depended on the task being performed (e.g. measuring eggs or checking for hatch). We used flushing distance as a measure of nest defence in the following analyses as the length of time observers subsequently spent at the nest cannot have affected it.

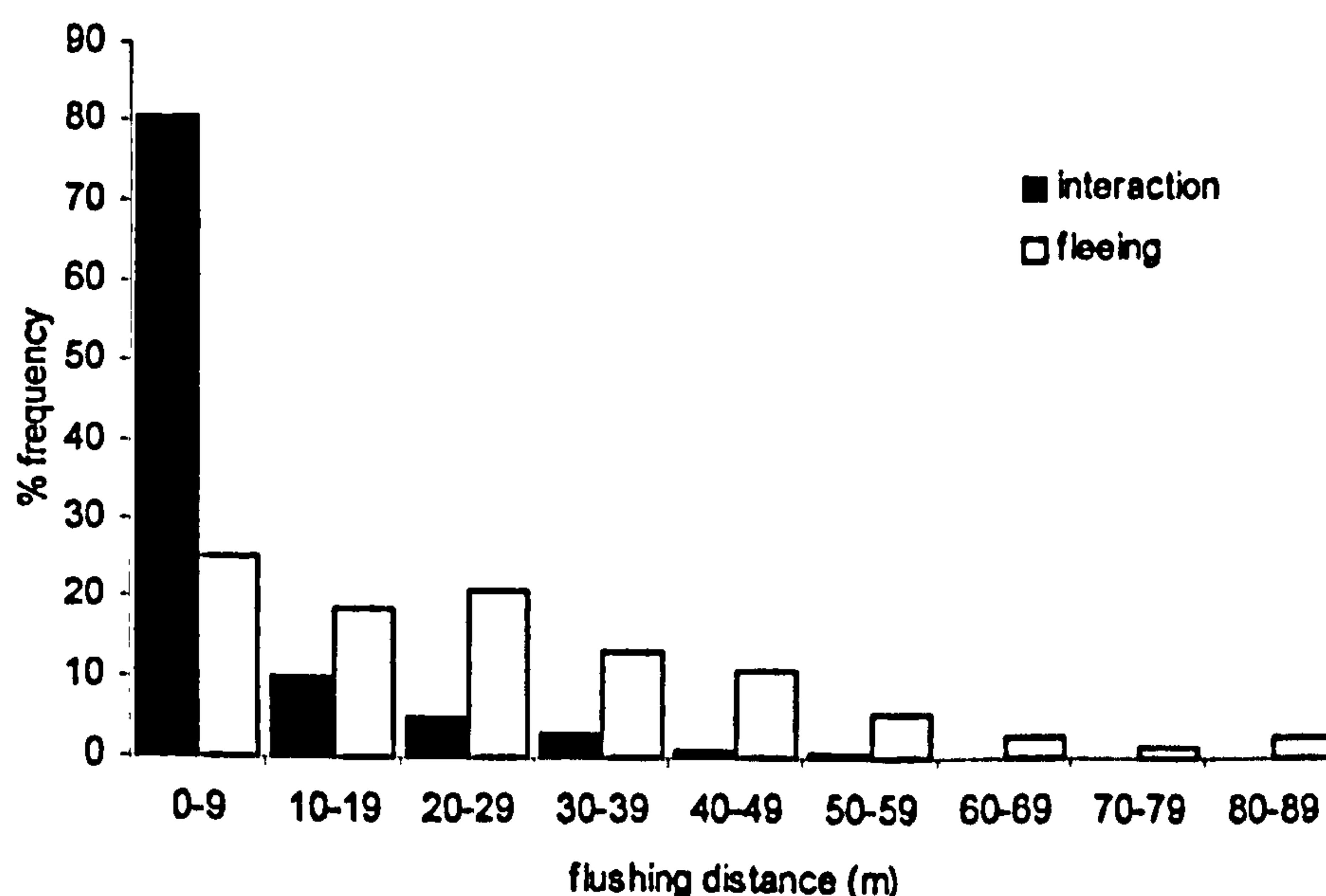


Figure 1. Variation in response type with flushing distance

### Egg-predation Risk

We compared the daily probability of clutch-predation at nests where the dotterel fled at least once to those where the dotterel always made an interaction response (following Byrkjedal, 1987). We compared within site-years only, as the abundance and species of predators and, consequently, the risk of predation varied between sites and years (Holt & Whitfield 1996a; Holt & Whitfield 1996b; Holt & Whitfield 1996c; D.P. Whitfield unpublished data). We used only site-years where at least an estimated 20% of clutches were depredated and where there were at least 120 monitored nest days from 12 or more nests. Using each pair of site-year estimates as a datum, we found no significant difference in the estimated daily probability of clutch-predation between nests where dotterel fled at least once and those where they always made an interaction response (Wilcoxon matched pairs:  $Z=0.000$ ,  $N=7$ ,  $P=1.000$ , Fig. 2).

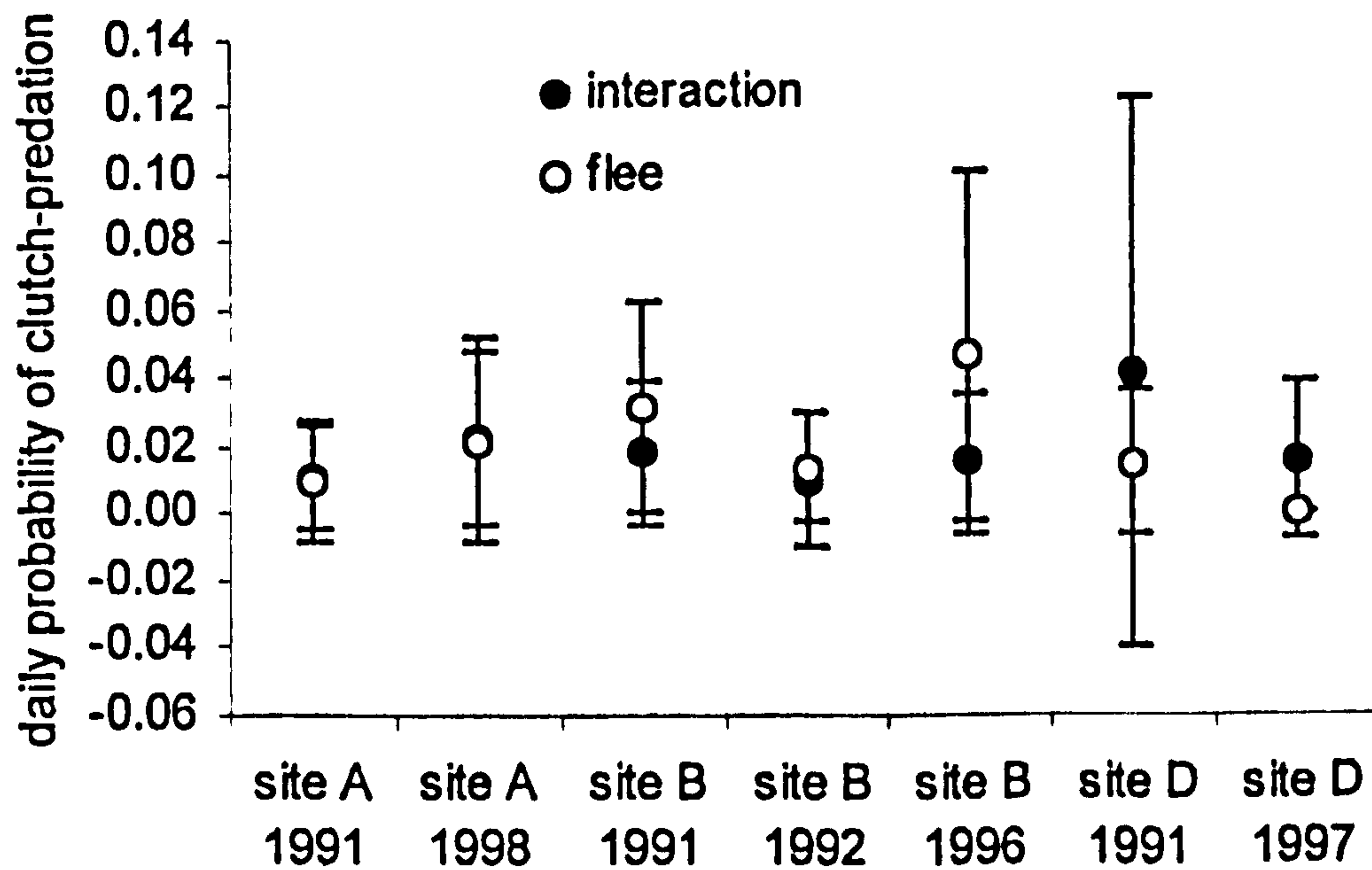


Figure 2. Daily probability of clutch-predation  $\pm$  95%CL (calculated according to Johnson 1979) comparing nests where dotterel made at least one fleeing response to those where dotterel always made interaction responses.

#### Trade-off Between Parent and Offspring Reproductive Value

We compared the log(square root) transformed flushing distances of individuals at the same nest at different stages of breeding. There were no significant differences between any of the stages (Table 1).

Table 1. Paired *t*-tests comparing log(square root) transformed flushing distances of individuals at the same nest at different stages of breeding. Early and late flushing distances were at least 12 days apart (i.e. over half the 23 day period from clutch completion to the start of hatch, Cramp & Simmons 1983) on completed, not hatching clutches. Hatching clutches were starred or pipped. In the comparison between 'with chick/s' and 'with no chicks', 'no chicks' included hatching clutches

Stages compared	<i>t</i>	<i>df</i>	<i>P</i>	Mean difference in flushing distance (earlier stage minus later stage)
Laying v. completed	-1.43	50	0.159	-0.6m
Early v. late completed, not hatching	0.34	63	0.733	0.0m
Not hatching v. hatching (no chicks)	1.08	46	0.284	0.0m
No chicks v. with chick/s	0.86	32	0.395	0.0m

We investigated the effect of parental age on individuals' nest-mean flushing distances, corrected for the effects of first egg date, altitude and the site\*year interaction using the general linear model (GLM) described in the following section. Since the number of individuals used in the calculation of site\*year parameters was sometimes small and the influence of one individual large, the residual value for an individual was calculated from a GLM that excluded it. Individuals' residual log transformed nest-mean flushing distances did not differ significantly between breeding attempts at least three years apart (paired *t*-test:  $t_{16}=0.238$ ,  $P=0.815$ , a mean of 0.5m greater when younger). Individuals were a median of three years older at the later nest, when they were a median of at least six years old.

In the following GLM (Table 2), flushing distance was found to significantly increase with first egg date. Substituting mean values for the rest of the terms in the minimal model, nest-mean flushing distance was predicted to increase by six metres over the 77d range of first egg dates.



Table 2. GLM testing the effects of environmental variables on log transformed nest-mean flushing distance (partial  $R^2$  quoted from the minimal model excluding the non-significant effect of human abundance)

source	Df	F	P	partial $R^2$ in the minimal model
intercept	1,249.8	14.14	0.000	
first egg date	1,249	7.87	0.005	0.028
altitude	1,249	6.59	0.011	0.031
human abundance	1,249	1.35	0.246	
year	7,20.3	0.31	0.942	
site	7,26.2	0.93	0.499	
site*year	20,249	2.651	0.000	0.171

### Environmental Variables

We tested whether a number of environmental variables affected log transformed nest-mean flushing distance using GLM. We entered site and year into the model as random factors and first egg date, altitude and the abundance of people as covariates. First egg date, altitude and the site\*year interaction term significantly affected flushing distance (Table 2). The abundance of people was excluded from the minimal model but site and year, although also non-significant, were retained as main effects for their significant interaction term. Substituting mean values for the rest of the terms in the minimal model, nest-mean flushing distance was predicted to decrease by 14m over the 470m range of nest altitudes.

We compared the log (square root) transformed flushing distances of an individual with the same nest in poorer and better weather. The better weather was at least 4°C warmer and not more than an estimated 2.1ms<sup>-1</sup> windier at 10m above ground level than the poorer weather. In all pairs, assuming that insolation and precipitation did not differ between the poorer and better weather, the estimated rate of egg cooling (Chapter 3) was greater in the poorer weather. Individual dotterel flushed at significantly shorter distances in poorer weather (paired *t*-test:  $t_{27}=2.176$ ,  $P=0.038$ , flushing distance a mean of 3.9m greater during the better weather).

We compared the log transformed mean flushing distances of an individual at the same nest before and during the emergence period of adult *Tipula montana*. Data for this test came from site A (1998), site B (1990, 1992, 1996) and site D (1991, 1998) where nest defence data

were available and where there were *T. montana* emergences whose duration was accurately recorded. As the abundance of *T. montana* was only recorded approximately every three days, to ensure correct classification, we only included nest defence records at least three days from the recorded start or end of the emergence period. There was an almost significant trend for mean flushing distances of individual dotterel to be greater during the emergence of adult *T. montana* than before it (paired *t*-test:  $t_{16}=2.102$ ,  $P=0.052$ , flushing distance a mean of 8.5m greater during the emergence). This increase in flushing distance was not a consequence of increasing temperature since, using the temperature recorded on site A as an index of weather on other sites, there was no significant difference in the mean shaded air temperature during nest defence responses before and during the *T. montana* emergence ( $t_{14}=0.947$ ,  $P=0.36$ , shaded air temperature was a mean of 1.1°C warmer during nest defence responses before the emergence, data for two nests missing as the AWS was not functioning). The increase in flushing distance was probably not a consequence of other seasonal effects as the mean dates of nest defence responses before and during the emergence were similar to those in the test comparing the flushing distance of individuals early and late in incubation, where no difference in flushing distance was found (mean dates: before emergence 7<sup>th</sup> June, early in incubation 5<sup>th</sup> June, during emergence 23<sup>rd</sup> June, late in incubation 22<sup>nd</sup> June).

### **Experience of People**

We were unable to test experimentally whether the number of prior human visits to the nest affected flushing distance as we did not want to increase disturbance above that necessary for nest monitoring. The opportunistic data on the number of nest visits are probably biased, since it is likely that individuals that flushed at longer distances would be flushed more frequently by us and by other people visiting the study sites.

Instead, we investigated whether the abundance of people in the study site (in the above GLM) and proximity to a path affected flushing distance. We compared the log-transformed nest-mean flushing distances of dotterel nesting close to and far from paths on site A. Site A was heavily visited by people in all years, receiving roughly 100 visitors per day, most of

whom used paths (Amphlett 1995). There was no significant difference in the log transformed nest-mean flushing distances of dotterel nesting less than or equal to 70m from a path and those nesting more than 410m from a path ( $t$ -test:  $t_{25}=1.650$ ,  $P=0.111$ , mean flushing distance close to path=1.4m, far from path=1.3m). There was also no significant difference in the log transformed nest-mean flushing distances of the same individuals when they nested closer to and further from paths (paired  $t$ -test:  $t_{10}=0.480$ ,  $P=0.641$ , residual flushing distance a mean of 0.7m greater when further from a path). In this paired test individuals' nests were within 120m of a path when classed as 'closer' or more than 120m when 'further' and individuals with 'closer' nests were a mean of 230m closer to a path than their 'further' nest. To ensure the independence of the results of this test and the previous test, no recognisable individuals were included in both tests. We cannot predict the proximity to a busy path that may influence dotterels behaviour and, in both these tests, the distances from a path used to categorise nests as near or far were chosen to maximise small sample sizes.

### **Variation Between Individuals**

We corrected individuals' nest-mean flushing distances for the effects of first egg date, altitude and the site\*year interaction in the same way as when testing for an effect of age. Confining the sample to individuals with data for more than one nest, we tested whether individuals differed in their nest-mean flushing distance using GLM, entering individual identity as a random factor. As error variances between individuals were unequal we give jackknifed estimates of  $F$  and partial  $R^2$ , which were log and arcsine transformed, respectively (Sokal & Rohlf 1981). Individuals' log transformed residual flushing distances significantly differed (GLM:  $F_{46,92}=3.322$ ,  $P<0.001$ , partial  $R^2 \pm 95\% \text{ C.L.} = 0.629 \pm 0.035$ ). Differences between individuals accounted for an estimated 63% of variation in nest-mean flushing distance after controlling for first egg date, altitude and the site\*year effect, or an estimated 48% before controlling for any other variables.

## **DISCUSSION**

We found no evidence that dotterel changed their flushing distances in response to our measures of their experience of people. Although of low statistical power, the test of the effect of human visits to the site and the comparisons of dotterel nesting close and far from paths suggested no consistent trend in flushing distance with experience of the simulated predator. We can assume that variation in dotterel's experience of humans did not confound the results of other analyses.

The four measures of the nest defence response were related. Dotterel that flushed at shorter distances were more likely to make an interaction response, move a shorter distance from the nest and approach closer to the nest. This type of response brought the dotterel into closer proximity with the simulated predator. Dotterel should only make this riskier kind of response if it carries a sufficiently higher effectiveness in defence of the nest (Andersson et al. 1980), or when the costs are sufficiently less. The relative effectiveness of the different responses is not clear. Byrkjedal (1987) found that, in Norway, dotterel that fled at least once were less likely to lose their nest to a predator than those that always interacted. However, we found no trend in this study. The effectiveness of different nest defence behaviours may have varied between the studies because of different predator suites.

While it is unclear if the different dotterel nest defence responses were generally associated with differences in clutch losses to predators, they probably carried different costs in terms of egg-exposure. Dotterel's breeding grounds are cool, windy and wet so that eggs exposed when the parent leaves the nest will cool rapidly. Dotterel breed in dwarf vegetation in an open habitat where they have a relatively good view of the surrounding ground and airspace (Chapter 6) and so have a relatively high probability of seeing any predators within a large area. The probability of a bird flushing to a randomly moving predator (i.e. one that has not seen the nest) is proportional to its flushing distance to that predator, so individuals with longer flushing distances will flush from the nest more frequently. In addition, dotterel that flushed at longer distances stayed further from the nest, so may take longer to return.

Therefore, the frequency and duration of egg exposure is likely to vary with flushing distance. While the exposure of eggs during a single flush from the nest might be unimportant, if predators are seen relatively frequently, the cumulative cost of exposure during numerous flushes might be high. An individual may vary egg exposure by varying the distance of the potential predator from the nest at which it flushes. We found that dotterel varied their nest defence responses with the cost of egg exposure: dotterel flushed at shorter distances in poorer weather and at higher altitudes when eggs would have cooled faster and to lower temperatures. The principal, potential costs of egg cooling are damage to the embryos, extension of the incubation period and increased energetic costs for the parent. Prolonged exposure to low temperatures may kill the embryo or have detrimental sublethal effects (Batt & Cornwell 1972; Webb 1987). It is unlikely that egg cooling as a result of nest defence responses will kill or severely harm dotterel embryos, as they embryos can successfully hatch and fledge after numerous bouts of exposure at low temperatures for several hours (Chapter 4). The second potential cost of egg cooling is that embryos will spend more time below their physiological zero temperature (PZT), reducing their overall rate of development and extending the incubation period (Haftorn 1988; Tombre & Erikstad 1996; Chapter 4). Longer incubation periods are likely to reduce the probability of embryos surviving until hatch (Tombre & Erikstad 1996). Dotterel may have reduced their flushing distances in poorer weather to avoid extension of the incubation period. However, before the clutch is completed nest attendance is low (Kálás 1986), so dotterel do not appear to be minimising time that embryos spend below the PZT at this stage. Dotterel should, then, flush at shorter distances once the clutch is completed, when we hypothesise that they are adjusting nest defence to reduce time below the PZT, than when the clutch is incomplete. Since flushing distance did not differ between complete and incomplete clutches we can tentatively reject extension of the incubation period as the reason underlying variation in flushing distance with weather conditions. The last potential cost of greater egg cooling is increased parental energetic costs. When the parent returns to the eggs that have cooled as a result of a nest defence response it must re-warm them, which can be energetically costly (Biebach 1986). Birds may defray some of the egg-rewarming costs associated with flushing by spending the time off the nest feeding. However, unless dotterel were kept off the nest for relatively long periods they did not

appear to feed very much. As uniparental incubators in a cool climate, dotterel's energetic expenditure is likely to be high (Piersma & Morrison 1994; Tulp et al. 1998) and their feeding time constrained (Drent et al. 1985; Kálás 1986), so that minimisation of energetic costs such as those incurred during nest defence responses is likely to be important. Dotterel tended to flush at greater distances during the adult emergence period of an important prey, the crane fly *Tipula montana*, than before it. Thus, dotterel tended to increase their flushing distances in better feeding conditions, when their energetic expenditure for nest defence would have been less constrained. This suggests that it is the energetic costs of re-warming the eggs, rather than the effects of cooling on the embryos or incubation period, that causes dotterel to reduce egg exposure in poorer weather.

Dotterel did not vary their nest responses in relation to two of the three life history theory predictions: flushing distance did not differ between stages of breeding or with the parent's age, but dotterel did increase their flushing distances at nests initiated later in the season. The life-history theory predictions rest upon a trade-off of changes in the parent's and offspring's reproductive values as a consequence of nest defence. Since we found no clear evidence of a relationship between flushing distance and the risk of clutch predation, our life-history theory predictions are invalidated. Additionally, it is difficult to interpret whether longer or shorter flushing distances represent greater parental investment since, although long flushing distances appear to incur greater energetic costs, short flushing distances bring the parent into closer proximity to a potentially dangerous predator. Many studies interpret shorter flushing distance and increased interaction with a 'predator' as an increase in parental investment (e.g. Myers 1978; Andersson et al. 1980; Reid & Montgomerie 1985; Dale et al. 1996) and the distraction displays associated with shorter flushing distances may be physiologically stressful (Graul 1975). We predicted, from life history theory, that investment in nest defence should increase with the parent's age but, if survival rates or fecundity only start to decline with great age, then we would expect little reduction in an individual's residual reproductive output over the three years minimum age difference in our sample. The most common pattern in shorebirds appears to be relatively little variation in mortality rates with age after the first year, as seen in dunlin *Calidris alpina*, northern lapwing *Vanellus vanellus*,

common redshank *Tringa totanus* and Eurasian oystercatcher *Haematopus ostralegus* (Soikkeli 1967; reviewed in Hildén 1977; Goss-Custard et al. 1982; Peach et al. 1994; Insley et al. 1997) but survivorship declines rapidly with age in Temminck's Stint *Calidris temminckii* (Hildén 1977) and may increase with age in common redshank *Tringa totanus* (reviewed in Hildén 1977). However, some of these studies are limited to relatively young birds or did not control for age-dependent site fidelity and, without further data for older individuals, increasing mortality with great age might not be detectable (Botkin & Miller 1974; Hildén 1977; Newton 1989). Without knowing the pattern of dotterel senescence we cannot be sure that the reduction in residual reproductive value with age is sufficient to predict detectable variation in parental investment in nest defence. Although the life-history theory prediction of parental investment increasing through the season may not be valid, flushing distance was greater at nests initiated later in the season. Alternative hypotheses to explain this may be that, as weather conditions and/or food availability improved through the breeding season, longer flushing distances became less costly or dotterel's energetic expenditure became less constrained, or that parents initiating nests later in the season began incubation in better body condition.

We could not account for all of the variation in nest-mean flushing distances between sites and years. The costs of different responses may vary between sites and years (e.g. local weather) or the ability of birds to meet costs may vary (e.g. different food availability). The model of the effects of altitude, first egg date, year and site on flushing distance accounted for only a relatively small proportion (23%) of variation. We can probably attribute some of the remainder to variation within individuals through changes in weather conditions and food abundance, leading to poor estimates of nest-mean flushing distance. After controlling for altitude, first egg date, year and site, differences between individuals accounted for an estimated 63% of variation in nest-mean flushing distances, or 48% of variation in nest-mean flushing distances overall. We can only speculate on the reasons for this large variation between individuals. If predators adopted search strategies for nests (e.g. looking for fleeing parents or exposed eggs) any consequent frequency dependent risk of egg-predation for the different responses would favour varied responses. Alternatively, if an individual's response is

constrained by its ability to bear the energetic costs of the response, then variation between individuals' responses might result from differing individual quality. Energetic costs for the same response might vary between individuals if they differ, for example, in their nest construction or nest site selection. Alternatively, the effectiveness of responses may differ between individuals if variation in their plumage, behaviour, or nest characteristics (Montgomerie & Weatherhead 1988; Sproat & Ritchison 1993) affect their conspicuousness. Lastly, if there is a genetic basis to variation in nest defence and the effectiveness of different types of nest defence varies spatially, then the large scale dispersal (Thompson & Whitfield 1993; D.P. Whitfield unpublished data) and so gene-flow in dotterel may prevent individuals' nest defence from conforming to a local optimum (Greenwood & Harvey 1982).

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## REFERENCES

- Amat, J.A., Carrascal, L.M. & Moreno, J. 1996. Nest defense by chinstrap-penguins *Pygoscelis antarctica* in relation to offspring number and age. Journal of Avian Biology , 27, 177-179.
- Amphlett, A. 1995. Cairn Gorm Ben Macdui plateau visitor survey, May August, 1992-1994. Edinburgh: Royal Society for the Protection of Birds
- Andersson, M., Wiklund, C.G. & Rundgren, H. 1980. Parental defence of offspring: a model and an example. Animal Behaviour , 28, 536-542.
- Barash, D.P. 1975. Evolutionary aspects of parental behaviour: distraction behaviour of the Alpine Accentor. Wilson Bulletin , 87, 367-373.



- Batt,B.D. & Cornwell,G.W. 1972. The effects of cold on Mallard embryos. Journal of Wildlife Management , 36, 745-751.
- Biebach,H. 1986. Energetics of rewarming a clutch in Starlings (*Stumus vulgaris*). Physiological Zoology , 59, 69-75.
- Botkin,D.B. & Miller,R.S. 1974. Mortality rates and survival of birds. American Naturalist , 108, 181-192.
- Byrkjedal,I. 1987. Antipredator behaviour and breeding success in Greater Golden Plover and Eurasian Dotterel. The Condor , 89, 40-47.
- Cramp,S. & Simmons,K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic: Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Dale,S., Gustavsen,R. & Slagsvold,T. 1996. Risk-taking during parental care - a test of 3 hypotheses applied to the pied flycatcher. Behavioral Ecology And Sociobiology , 39, 31-42.
- Drent,R.H., Tinbergen,J.M. & Biebach,H. 1985. Incubation in the Starling, *Stumus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands Journal of Zoology , 35, 103-123.
- East,M. 1981. Alarm calling and parental investment in the Robin *Erithacus rubecula*. Ibis , 123, 223-230.
- Galbraith,H., Murray,S., Duncan,K., Smith,R., Whitfield,D.P. & Thompson,D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. Ibis , 135, 148-155.
- Geiger,R., Aron,R.H.& Todhunter,P. 1995. The Climate Near the Ground. 5 edn. Braunschweig: Vieweg.
- Goss-Custard,J.D., Le V.Dit Durrell,S.E.A., Sitters,H.P. & Swinfen,R. 1982. Age-structure and survival of a wintering population of Oystercatchers. Bird Study , 29, 83-98.
- Gramza,A. 1967. Responses of brooding nighthawks to a disturbance stimulus. Auk , 84, 72-86.
- Graul,W.D. 1975. Breeding biology of the Mountain Plover. Wilson Bulletin , 87, 6-31.

- Greenwood,P.J. & Harvey,P.H. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics , 13, 1-23.
- Greig-Smith,P.W. 1980. Parental investment in nest defence by Stonechats (*Saxicola torquata*). Animal Behaviour , 28, 604-619.
- Haftorn,S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Ornis Scandinavica , 19, 97-110.
- Hatch,M.I. 1997. Variation in song sparrow nest defense: individual consistency and relationship to nest success. The Condor , 99, 282-289.
- Hildén,O. 1977. Population dynamics in Temminck's stint *Calidris temminckii*. Oikos , 30, 17-28.
- HMSO 1982. Observer's Handbook. 4th edn. London: HMSO.
- Holt,S. & Whitfield,D.P. 1996a. Montane Ecology Project report series: [site A].  
Edinburgh: Scottish Natural Heritage
- Holt,S. & Whitfield,D.P. 1996b. Montane Ecology Project site report series: [site B].  
Edinburgh: Scottish Natural Heritage
- Holt,S. & Whitfield,D.P. 1996c. Montane Ecology Project site report series: [site C].  
Edinburgh: Scottish Natural Heritage
- Horsfield & Thompson 1996. The uplands: guidance on terminology regarding altitudinal zonation and related terms. Information and Advisory Note No. 26. Scottish Natural Heritage, Battleby, UK.
- Insley,H., Peach,W.J., Swann,B. & Etheridge,B. 1997. Survival rates of Redshank *Tringa totanus* wintering on the Moray Firth. Bird Study , 44, 277-289.
- Johnson,D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk , 96, 651-661.
- Kálás,J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Kersten,M. & Piersma,T. 1986. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. Ardea , 75, 175-188.

- King, D.I. 1999. Mortality of an adult Veery incurred during the defence of nestlings. Wilson Bulletin , 111, 576-577.
- Knight, R.L. & Temple, S.A. 1986. Why does intensity of avian nest defence increase during the nesting cycle? Auk , 103, 318-327.
- Komdeur, J. & Kats, R.K.H. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. Behavioural Ecology , 10, 648-658.
- Larson, S. 1960. On the influence of the Arctic Fox (*Alopex lagopus*) on the distribution of Arctic birds. Oikos , 11, 277-305.
- McClatchey, J. 1996. Spatial and altitudinal gradients of climate in the Cairngorms- observations from climatological and automatic weather stations. Botanical Journal of Scotland , 48, 31-49.
- Montgomerie, R.D. & Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. Quarterly Review of Biology , 63, 167-187.
- Myers, J.P. 1978. One deleterious effect of mobbing in the Southern Lapwing (*Vanellus chilensis*). Auk , 95, 419
- Nethersole-Thompson, D. 1973. The Dotterel. Glasgow: Collins.
- Newton, I. 1989. Synthesis. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 441-470. London: Academic Press.
- Norusis, M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Gorinchem: SPSS Ltd.
- Patterson, T.L., Petrinovich, L. & James, D.K. 1980. Reproductive value and appropriateness of response to predators by White-crowned Sparrows. Behavioural Ecology and Sociobiology , 7, 227-231.
- Peach, W.J., Thompson, P.S. & Coulson, J.C. 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. Journal of Animal Ecology , 63, 60-70.
- Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.
- Regelmann, K. & Curio, E. 1983. Determinants of brood defence in the Great Tit *Parus major* L. Behavioural Ecology and Sociobiology , 13, 131-145.

- Reid, M.L. & Montgomerie, R.D. 1985. Seasonal patterns in nest defence by Baird's Sandpipers. Canadian Journal of Zoology , 63, 2207-2211.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. Smiths. Cont. Zool. 9, 1-48.
- Rytkönen, S., Koivula, K. & Orell, M. 1990. Temporal increase in nest defence intensity of the Willow Tit (*Parus montanus*): parental investment or methodological artifact? Behavioural Ecology and Sociobiology , 27, 283-286.
- Rytkönen, S., Orell, M., Koivula, K. & Soppela, M. 1995. Correlation between two components of parental investment - nest defense intensity and nestling provisioning effort of Willow Tits. Oecologia , 104, 386-393.
- Sjöberg, G. 1994. Factors affecting nest defense in female Canada Geese *Branta canadensis*. Ibis , 136, 129-135.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the the dunlin (*Calidris alpina*). Annales Zoologici Fennici , 4, 158-198.
- Sokal, R.R. & Rohlf, F.J. 1981. Biometry. 2 edn. New York: W. H. Freeman and Company.
- Sproat, T.M. & Ritchison, G. 1993. The nests defence behaviour of Eastern Screech-owls: effects of nest stage, sex, nest type and predator location. The Condor , 95, 288-296.
- Thompson, D.B.A. & Whitfield, D.P. 1993. Research Progress Report: Research on mountain birds and their habitats. Scottish Birds , 17, 1-8.
- Tombre, I.M. & Erikstad, K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Tulp, H., Schekkerman, H., Piersma, T., Jukema, J., de Goeij, P., & van de Kam, J. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. Zeist: WIWO
- Ueta, M. 1999. Cost of nest defense in Azure-winged Magpies. Journal of Avian Biology , 30, 326-328.
- Wallin, K. 1987. Defence as parental care in Tawny Owls (*Strix aluco*). Behaviour , 102, 213-230.
- Webb, D.R. 1987. Thermal tolerance of avian embryos: A review. The Condor , 89, 874-898.

- Westmoreland,D. 1989. Offspring age and nest defence in Mourning Doves: a test of two hypotheses. Animal Behaviour , 38, 1062-1066.
- Westneat,D.F. 1989. Intensity of nest defence in Indigo Buntings increases with stage and not number of visits. Auk , 106, 747-749.
- Whitfield,D.P. 1999. Methods for ageing Dotterel *Charadrius morinellus*. Ringing & Migration , 19, 200-204.
- Wiklund,C.G. 1990a. Offspring protection by Merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defence of young. Behavioural Ecology and Sociobiology , 26, 217-223.
- Wiklund,C.G. 1990b. The adaptive significance of nest defence in Merlin, *Falco columbarius*, males. Animal Behaviour , 40, 244-253.
- Wilkie,A.O.M. 1980. Incubation Behaviour of the Dotterel. In: Cambridge Norwegian Expedition 1978 Report (Ed. by J.L.Innes), pp. 34-58. Cambridge: Cambridge University.

## Chapter 8

# DOES THE PLUMAGE BRIGHTNESS OF MALE DOTTEREL INDICATE INCUBATION ABILITY?

Sue Holt, D. Philip Whitfield & David M. Bryant

### ABSTRACT

The Eurasian dotterel *Charadrius morinellus* has reversed sex roles and courting females prefer males with brighter plumage. Brighter plumage may be a honest signal of parental ability and, by choosing brighter males, females may be choosing males that are more likely to successfully incubate their eggs. However, we found no evidence that a male's plumage brightness indicated his incubation ability in terms of his nest attendance, his ability to successfully incubate through prolonged snow-lie or his level of body stores.

## INTRODUCTION

In the Eurasian dotterel *Charadrius morinellus* most breeding attempts are cared for by the male alone (Cramp & Simmons 1983; Kálás & Byrkjedal 1984). Like other sex-role reversed species, female dotterel have brighter plumage and are between 1% and 5% larger than males (depending on the body part measured), and are the more active sex in courtship (Kálás 1988 and references therein; Owens et al. 1994). In most breeding attempts, the female abandons the clutch to the male's sole care as soon as the clutch is completed, so the probable success of the breeding attempt depends heavily upon the male's parental ability. There is variation in the plumage brightness (most notably of the head, neck and belly markings) within the sexes (Owens et al. 1994) and female dotterel choose to pair with brighter males (Owens et al. 1994). If a male's plumage brightness indicates his quality as a parent during the incubation period, females may be choosing brighter males because they are more likely to successfully hatch their eggs (Owens et al. 1994).

In this study we test whether male dotterels' plumage brightness is an honest indicator of their incubation ability in three ways. Dotterel nests that are incubated less take longer to hatch (Chapter 4). An extended incubation period may decrease the success of the breeding attempt in several ways: longer incubation periods may increase the risk of the clutch being lost as the probability of loss is a usually function of time (Mayfield 1961), males may further deplete their body reserves constraining their investment in incubation or care of the chicks, and later hatched chicks may have smaller yolk reserves and reduced fledging success (Perrins 1965; Arcese & Smith 1985; Martin 1987; Hepp et al. 1990; Siikamaki 1995; Tombre & Erikstad 1996; Williams 1996). We test whether brighter males had higher nest attendance which should have minimised their incubation periods.

Uniparental incubators can experience periods of energetic constraint (Chapter 3, Haftorn 1988), but these may only result in reduced hatching success during snowstorms (reviewed in Cartar & Montgomerie 1985) or prolonged periods of poor weather (Kondratiev 1982). Therefore, differences in the incubation ability between individuals may only become apparent during periods of extreme constraint such as snowstorms. After snowfalls on dotterel's

breeding grounds, snow cover may increase to 100% and may persist for several days (D.P. Whitfield unpublished data), during which time food may be covered by snow and thermodynamic costs may be increased by low temperatures (Wiersma & Piersma 1994; Andreev 1999). Some dotterel permanently deserted their clutches during prolonged periods of snow-lie (Thompson & Whitfield 1993; Owens et al. 1994) and we test whether brighter males were more likely to continue incubation through these periods.

Higher nest attendance is associated with greater body stores in dotterel (Chapter 3) and other shorebirds (Hegyí & Sasvári 1998): body stores may provide an energetic buffer during periods of high energetic demands or low food availability, allowing higher nest attendance and increasing the probability of successful incubation (Hohman 1986; Moreno 1989; Hepp et al. 1990). We test whether brighter males had greater body stores.

## **METHODS**

Data on plumage scores and body stores were collected between 1989 and 1998 on seven sites in the Central Highlands of Scotland. Dotterel are vulnerable to illegal egg collectors so site names are not given. All observers were licensed to disturb nesting dotterel.

Dotterel were plumage scored in the field from 1990 on a scale that ran from one to six, according to Owens (1991) and from 1987 to 1989 on a scale of one to five adapted from Kálás (1988). A high score on either scale indicated brighter plumage. Dotterel were caught in walk-in traps or with single-shelf mist nets and mass was measured to 0.5 g using spring balances and wing length (maximal chord) to 0.5 mm on a stopped wing rule (there was no significant differences between observers measures of wing length, D. P. Whitfield unpublished data). To estimate an individual's body stores we corrected mass for body size (wing length) and for the factors that affected the state of depletion of body reserves (stage of incubation, availability of *Tipula montana*, parental care and site, Holt et al. 2002). Trapped dotterel were given individual colour-ring combinations. We sexed dotterel in the field using plumage characters (Kálás 1988; Owens 1991).



Data on incubation scheduling were collected in 1997 and 1998 from two sites, separated by 8km. Nest attendance was recorded using small temperature probes at the centre of nests attached to Tinytag dataloggers (Gemini Data Loggers (UK) Ltd, Chichester, UK).

The date that a clutch was initiated (first egg date) was observed, estimated from hatch date (assuming a 28 day period from first egg laid to last chick hatched, Cramp & Simmons 1983), D.P. Whitfield unpublished data) or estimated from an equation relating egg density to days until hatch (derived from measurements of clutches of known hatch date, D.P. Whitfield unpublished data).

Adults of the crane fly species *Tipula montana* are relatively large and energy rich and slow moving and, during the typically 3-week emergence period, very abundant. *T. montana* have a two year life-cycle, emerging as adults in the second year (D.P. Whitfield unpublished data). On some sites, adult emergence is synchronised, resulting in alternating years with and without adult emergences (Galbraith et al. 1993; D.P. Whitfield unpublished). When available, *T. montana* form an important part of dotterels' diet (Galbraith et al. 1993). We measured the abundance of adult *T. montana* from transects. Approximately every three days, the observer slowly walked five to ten 10 m transects at random locations in areas used by feeding dotterel and counted the number of adult *T. montana* seen in a 2 m band centred along each transect. Additionally, the number of adult *T. montana* trapped in water baths was counted approximately every three days for some years on sites A, B and C; in 1990, water baths provided the only abundance data for site E (two baths were placed in a typical stand of each major plant community). On site A the total number of adult *T. montana* seen per day was also estimated and recorded on a log scale (0, 1-10, 11-100, 101-1000, >1000). An emergence was taken to start and finish when the first and last adult *T. montana* was recorded by any of these methods. When an adult emergence was observed the earlier availability of pre-emergence larvae could be assumed from their life-cycle.

Statistical tests were carried out using SPSS (Norusis 1990). Two-tailed probabilities are given. Means are quoted  $\pm$  95% confidence limits.

## RESULTS

### Plumage brightness and nest attendance

There was no significant difference in nest attendance comparing brighter and duller uniparental dotterel incubating at the same time on the same site (paired t-test:  $T_{13}=0.131$ ,  $P=0.898$ , brighter males attended  $0.3\% \pm 4.3\%$  more of the time than their paired duller males,  $8.3 \pm 2.9$  days attendance compared in pairs). Similarly, there was no significant association between plumage score and the coefficient for nest attendance (estimated from a GLM of nest attendance that controlled for the effects of past and current energetic costs, *Tipula montana* availability and stage of incubation in Chapter 3, Spearman's rank correlation:  $r_s=0.209$ ,  $N=27$ ,  $P=0.296$ , using only uniparental dotterel that initiated clutches in May to control for any seasonal effects in plumage brightness).

### Plumage brightness and snow desertion

There was no evidence that uniparental male dotterel with brighter plumage were less likely to desert during snow lie than duller males (Table 1, in four of five years deserting males had higher mean plumage score ranks than males that did not desert, sign test exact  $P=0.375$ ,  $N=5$ ). We compared only plumage scores within the same year (as the coverage and duration of snow lie differed between years and the method of plumage scoring changed in 1990) and used only data from site A as prolonged snow lie and consequent desertions were rare on other study sites.

Table 1. Plumage score and the rate of snow desertion.

year	plumage score	number of nests		median plumage score		Mann-Whitney test		mean rank	
		deserted during snow	not deserted during snow lie	deserted during snow lie	not deserted during snow lie	U	P (exact)	deserted during snow lie	not deserted during snow lie
1987	2	0	2	3	2	0.0	0.667	3.00	1.50
	3	1	0						
1989	2	0	1	3	3	18.5	0.491	8.42	6.81
	2.5	1	2						
	3	5	5						
1990	2	1	3	3	3	32.0	0.961	9.17	8.91
	3	5	7						
	4	0	1						
1991	2	1	1	3	3	10.5	0.469	5.50	7.45
	3	2	8						
	4	0	1						
1998	2.5	1	1	3	2.5	0.5	0.500	2.83	1.50
	3	2	0						

### Plumage brightness and body stores

There was no evidence that plumage score and body stores were associated (Spearman's rank correlation of mass residualised for site, days since first egg date, *Tipula montana* availability and wing length with plumage score: 1987 – 1989,  $r_s=0.013$ ,  $N=29$ ,  $P=0.946$ ; from 1990,  $r_s=0.014$ ,  $N=73$ ,  $P=0.909$ , using only uniparental males with clutches initiated in May to control for any seasonal variation in plumage brightness). There was also no significant association between plumage score and body stores if we corrected mass only for body size to obtain a measure of body stores (Spearman's rank correlation of mass residualised for wing length: 1987 – 1989,  $r_s=0.163$ ,  $N=30$ ,  $P=0.388$ ; from 1990,  $r_s=0.118$ ,  $N=81$ ,  $P=0.294$ , using only uniparental males with clutches initiated in May to control for any seasonal variation in plumage brightness).

Within individuals, there was also no evidence that residual mass increased with plumage score, although the sample size was very small (comparing the residual masses of individuals in years when they had brighter plumage with years when they had duller plumage, T test:  $T_6=0.590$ ,  $P=0.577$ , residual mass was  $2.1 \pm 6.8$ g less when brighter).

## DISCUSSION

We found no evidence that a male dotterel's plumage score indicated its incubation ability, in terms of nest attendance, susceptibility to desert during prolonged snow-lie or amount of body stores.

There was no association between plumage brightness and physical condition in male sex-role reversed red-necked phalaropes *Phalaropus lobatus* (Reynolds 1987) but Owens (1991; 1994) found that brighter male Eurasian dotterel had greater body stores, higher nest attendance and were better able to successfully incubate through prolonged snow-lie. Owens data probably had the advantage over this study of less variation in estimates of plumage brightness due to different observers and different study sites, but his sample sizes were smaller, although replicated in the analysis of body stores. This study controlled for a greater number of influential factors to obtain better estimates of body stores and nest attendance. Owens (1994) corrected plumage scores for the effect of age although there was no significant effect of age on plumage brightness and the method used did not age birds correctly (Whitfield 1999): this may have introduced bias into the data. In this study we did not correct plumage scores for age as, although individual's plumage scored varied between years there appeared to be no consistent trend to become brighter or duller with age (D.P. Whitfield unpublished data). Although we cannot definitely evaluate whether our lack of any significant results is likely to be a Type II error or Owens' significant results are likely to be a Type I error, this study had the advantages of larger sample sizes and better control of other influential factors.

If females do not prefer brighter males because of better incubation ability they may choose brighter males for other reasons: bright males may be better at fledging the chicks once hatched or, if plumage brightness is heritable, they may give the female brighter, more attractive offspring, or her offspring may inherit advantageous traits linked associated with plumage brightness, such as a good immune system, better migratory ability or higher survival as chick or adult (Piersma & Jukema 1993; Norris 1993; Petrie 1994; Ryan 1997).

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## REFERENCES

- Andreev, A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich, 70, 13-22.
- Arcese, P. & Smith, J.N.M. 1985. Phenotypic correlates and ecological consequence of dominance in Song Sparrows. Journal of Animal Ecology, 54, 817-830.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour, 95, 261-289.
- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic: Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D.P. & Thompson, D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. Ibis, 135, 148-155.

- Haftorn,S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Ornis Scandinavica, 19, 97-110.
- Hegyí,Z. & Sasvári,L. 1998. Parental condition and breeding effort in waders. Journal of Animal Ecology , 67, 41-53.
- Hepp,G.R., Kennamer,R.A. & Harvey,W.F. 1990. Incubation as a reproductive cost in Wood Ducks. Auk , 107, 756-764.
- Hohman,W.L. 1986. Incubation rhythms of Ring-necked Ducks. The Condor , 88, 290-296.
- Holt,S., Whitfield,D.P., Duncan,K., Rae,S. & Smith,R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? Journal of Avian Biology , 33, 219-224
- Kálás,J.A. 1988. Sexual dimorphism in size and plumage of the polyandrous Dotterel (*Charadrius morinellus*): sex roles and constraints on sexual selection. Canadian Journal of Zoology , 66, 1334-1341.
- Kálás,J.A. & Byrkjedal,I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). Auk , 101, 838-847.
- Kondratiev,A.J. 1982. Biology of waders in the tundras of the north-east of Asia. Academy of Sciences of the USSR: Nauka, Moscow
- Martin,T.E. 1987. Food as a limit on breeding birds: a life history perspective. Annual Review of Ecology and Systematics , 18, 453-487.
- Mayfield,H. 1961. Nesting success calculated from exposure. Wilson Bulletin , 73, 255-261.
- Moreno,J. 1989. Strategies of mass change in breeding birds. Biological Journal of the Linnean Society , 37, 297-310.
- Norris,K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature , 362, 537-539.
- Norusis,M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Goringham: SPSS Ltd.
- Owens,I.P.F. 1991. Sexual selection in the sex-role reversed dotterel, *Charadrius morinellus*. PhD thesis, University of Leicester.
- Owens,I.P.F., Burke,T. & Thompson,D.B.A. 1994. Extraordinary sex roles in the Eurasian Dotterel: female mating arenas, female-female competition and female mate choice. American Naturalist , 144, 76-100.

- Perrins,C.M. 1965. Population fluctuations and clutch-size in the Great Tit *Parus major* L. Journal of Animal Ecology , 34, 601-647.
- Petrie,M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. Nature , 371, 598-599.
- Piersma,T. & Jukema,J. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the bar-tailed godwit. The Condor , 95, 163-177.
- Reynolds,J.D. 1987. Mating system and nesting biology of the red-necked phalarope *Phalaropus lobatus*: what constrains polyandry? Ibis , 129, 225-242.
- Ryan,M.J. 1997. Sexual selection and mate choice. In: Behavioural Ecology: an evolutionary approach (Ed. by J.R.Krebs & N.B.Davies), pp. 179-202. Oxford: Blackwell Science Ltd.
- Siikamaki,P. 1995. Are large clutches costly to incubate? - the case of the Pied Flycatcher. Journal of Avian Biology , 26, 76-80.
- Thompson,D.B.A. & Whitfield,D.P. 1993. Research Progress Report: Research on mountain birds and their habitats. Scottish Birds , 17, 1-8.
- Tombre,I.M. & Erikstad,K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Whitfield,D.P. 1999. Methods for ageing Dotterel *Charadrius morinellus*. Ringing & Migration, 19, 200-204.
- Wiersma,P. & Piersma,T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Williams,J.B. 1996. Energetics of avian incubation. In: Avian energetics and nutritional ecology (Ed. by C.Carey), pp. 375-415. New York: Chapman & Hall.

## Chapter 9

### GENERAL DISCUSSION

#### **Energetic constraint during incubation**

##### *How energetically costly was incubation?*

We estimated that the mean daily power for incubation over the whole day for uniparental incubators was  $0.97 \pm 0.03$ W, around 0.93 basal metabolic rate (BMR, estimated according to Kersten & Piersma 1986) and their modal daily power for incubation was 1.0 to 1.1W, which occurred on  $35 \pm 6\%$  of days (while sitting on the nest, they expended a mode of 1.2W to 1.3W or 1.2 to 1.3 times BMR).

Sitting at the mean ground temperature of  $7.2^\circ\text{C}$ , steady-state incubation cost dotterel an estimated 0.88W or 0.85 BMR. This compares with an estimated 1.2 BMR for dunlin *Calidris alpina* in the arctic (Ricklefs 1974) and between 0.5 and 0.95 BMR in a range of arctic breeding shorebirds (Andreev 1999). A colder arctic climate and dunlin's higher relative clutch mass (57% of body mass in dunlin, 43% in dotterel) may account for their higher estimated costs. Many past studies used biophysical models of heat exchange, such as Kendeigh's (1963), to estimate the energetic cost of incubation (Caldwell & Comwell 1975) but these biophysical models probably provide poor estimates (Croxall 1982; Walsberg 1983; Williams 1996) and generally estimate only the energetic cost of steady-state incubation although, in intermittent incubation, re-warming cooled eggs after a period of inattendant can be a large component of the overall energetic cost of incubation: dotterel's estimated energy expenditure while sitting, including the cost of egg rewarming, was 37% higher than if all time spent sitting was costed as steady-state incubation.

##### *Is incubation a significant energetic cost to dotterel?*

An energetic cost does not necessarily translate into a fitness cost: for a cost to be significant in evolutionary terms it must constrain the LRS of the individual. High energetic costs, as long



as they are below the metabolic ceiling (Drent & Daan 1980), or maximal thermogenesis in the case of thermostatic costs (Weiner 1992), may not limit LRS if energy can be abundantly supplied from large body reserves or a high intake of food. If an animal experiences energetic constraint at any stage of reproduction this may reduce the number of young that can be raised per breeding attempt if costs are proportional to the number of offspring produced (Thomson et al. 1998). Dotterel's investment of time and, sometimes, energy in incubation appeared to be limited by the degree of energetic constraint they experienced. Nest attendance declined as the potential cost of incubation increased, resulting in longer incubation periods and probably increasing the risk of nest failure (Tombre & Erikstad 1996) so it seems likely that the costs of incubation in dotterel may influence LRS.

Although dotterel may expend around 1.2 BMR on incubation alone while sitting, shorebirds' energy expenditure may be higher while off the nest than while sitting (Tulp et al. 1998). Similarly, although great tits *Parus major* had to increase their metabolic rate to keep their eggs warm, birds off the nest expended more energy than incubating birds (Mertens 1977). Restricted foraging time, even when the costs of incubation are very low, may mean that energetic constraint experienced during the incubation period limits the clutch size and, ultimately the number of young an individual can produce (Gabrielsen 1989; Erikstad & Tveraa 1995). But it is the combination of high energetic costs of incubation with restricted foraging time in which to recoup them that may place a uniparental incubator under severe energetic constraint. Uniparental incubators may improve their energetic balance by measures such as being fed by their mate or drawing on body reserves (Lyon & Montgomerie 1987; Smith et al. 1989; Moreno 1989a). Dotterel have an energetic advantage over the majority of uniparental species in which the female is the carer, in that they commence incubation with body reserves undepleted by egg production (Cartar & Montgomerie 1985), which may allow them to supplement their energy budget more greatly using reserves (although shorebirds may not draw upon body reserves for egg laying, Erckmann 1983).

Dotterel lost mass through the incubation period and this mass loss was a consequence of energetic constraint as they were heavier when assisted in incubation by a female or when

food was more abundant. Such depletion of body reserves may limit an individual's LRS by reducing its ability to invest in future breeding attempts or reducing its probability of surviving to breed again (Harris 1970; Hepp et al. 1990; Williams 1996; Erikstad et al. 1998). There is currently little information or consensus on how energetic costs compare between incubation and brood care in shorebirds in cold environments (review of data in Bryant & Tatner 1991; Heaney & Monaghan 1996) but, even if incubation is less energetically constrained than brood care, the observed depletion of body reserves during the incubation period in dotterel and other shorebirds would increase the degree of energetic constraint during chick rearing, further limiting LRS.

Further evidence of energetic constraint on LRS in dotterel is that nest attendance at uniparental nests appeared to be constrained by the balance between energetic costs and food intake, as attendance decreased when the current and past energetic costs of incubation and thermoregulation were higher and increased when food was more abundant. Reduced attendance is likely to reduce breeding success, principally by increasing the incubation period and, probably infrequently, by thermal damage to the embryos. In severe weather conditions, especially prolonged snow-lie, dotterel may neglect their eggs or permanently desert their clutches (Thompson & Whitfield 1993) so that energetic shortfall may lead to breeding failure or reduced breeding success.

Dotterels' nest defence behaviour also appeared to be under energetic constraint as dotterel flushed at longer distances under weather conditions when such a response was less energetically costly. The effect of variation in defence responses on the predation risk of the young is unclear but it is likely that it is riskier for the parent to flush from the nest at shorter distances that bring it into closer proximity to the predator. To conserve energetic expenditure, dotterel appeared to switch to a nest defence strategy that may have increased their risk of being depredated. Such compensatory reductions in energetic costs may negate any direct fitness consequences of energetic constraint but might themselves have deleterious fitness consequences, such as an increased risk of adult predation.

Egg neglect and variation in non-adaptive mass loss, incubation scheduling and nest defence all suggest that dotterel were energetically constrained during the incubation period, and that their behaviours change in response to temporal variation in the degree of constraint.

#### *Why do dotterel neglect their eggs?*

In very poor conditions birds, including dotterel, may neglect their eggs (Norton 1972; Morton & Pereyra 1985; Haftorn 1988). What causes birds to neglect their eggs? Incubating birds may be exceeding their maximum sustainable work limit, which may lie around four times BMR (Drent & Daan 1980) or their combined heat requirements for incubation and thermoregulation, after substitution from physiological processes, may exceed their maximal thermogenesis, which lies around six times BMR (Peterson et al. 1990). Alternatively, they may be below their work or thermogenesis maxima but a negative energy budget and depleted body reserves may compel them to spend time off the nest feeding (Croxall & Ricketts 1983).

Under still, dry conditions maximal thermogenesis is only achieved at temperatures far below those that breeding dotterel experienced (e.g. four *Calidris* species did not reach maximal thermogenesis at  $-20^{\circ}\text{C}$ , Norton 1973) so wind, precipitation and incubation would have greatly to increase a parent's heat loss for birds to have to abandon incubation because of insufficient thermogenesis. This may have been the cases, as the highest mean daily value for the index of the energetic cost of thermoregulation for dotterel was 4.6 times BMR, only allowing the addition of 1.4W for incubation before reaching maximal thermogenesis (although the index of the costs of thermoregulation does not supply absolute values as the effect of sitting in a nest on the cost of thermoregulation is unknown). As dotterel expended a mode of 1.2W to 1.3W while sitting, their total requirements for thermogenesis might have been around their maximal capacity in the poorest weather if they continued incubating.

Arctic shorebirds may frequently work above Drent & Daan's (1980) four times BMR maximum sustainable level of work (Piersma & Morrison 1994, Cresswell et al. unpubl.) so

an unsustainable level of energy expenditure may compel dotterel to abandon incubation to reduce energy expenditure. However, energy expenditure may usually be higher when off the nest than when incubating, (e.g. Mertens 1977; Tulp et al. 1998; Cresswell et al. unpubl.) so, to reduce energy expenditure, birds would probably have to behave differently during periods of neglect than during normal trips (e.g. roosting in a sheltered microclimate).

A dotterel's net energy budget did influence its incubation scheduling (e.g. nest attendance varied with food availability and the level of body reserves) so birds with severely constrained budgets might neglect their eggs. In summary, neither the maximum work level, maximal thermogenesis nor a constrained energy budget can be discounted as possible candidates for restricting a dotterel's investment of time and energy in incubation and causing egg neglect. Further work would be needed to determine which causes egg neglect. The doubly labelled water technique could be used to more accurately determine whether daily energy expenditure would have exceeded Drent & Daan's 4 x BMR when egg neglect occurred, although there is some doubt about the generality of this maximum (Bryant & Tatner 1991). Field metabolic chambers over incubating birds can be used to estimate the power used while sitting (Norton 1973) and could determine whether this exceeded maximal thermogenesis (although it is possible that shorebirds' maximal thermogenesis is different from the 6 x BMR values estimated from a range of mostly passerine species). Finally, if neglect ceased when the energy budget was positively manipulated with supplementary food, this would suggest that it is the net energy budget, rather than either of the maxima of energy expenditure that causes egg neglect.

### *Chilling tolerance of eggs*

This study set out to investigate some of the behaviours that dotterel may use to manage and reduce energetic costs during the incubation period. However, the evolution of the behaviour, physiology and morphology of a species are interdependent. When energetically constrained, dotterel neglected their eggs but this behaviour was only possible because of a physiological property of the embryos: their extreme tolerance of chilling. This physiological property may

be a prerequisite for uniparental care in dotterels' cold climate. When the demands for investment in reproduction exceed the parent's optimal level of investment, mechanisms such as egg neglect, chick chilling tolerance, brood reduction or a flexible chick growth rate may adjust demand to permit successful breeding (Eppley 1996; Erikstad et al. 1998). It is not yet possible to say whether dotterel embryos are especially chilling tolerant compared with other birds, but there is some anecdotal evidence to suggest that arctic shorebird embryos may also be tolerant of chilling (Norton 1972; Cartar & Montgomerie 1987).

*How does dotterel's nest attendance compare to other birds?*

Dotterels nest attendance was energetically constrained: does comparison of patterns of nest attendance rates within and between shorebird species and other groups also support energetic constraint? Estimates of uniparental dotterel's nest attendance, of between 73% and 89% (Wilkie 1981; Kálás 1986; Pulliainen & Saari 1994) lie within the range of values recorded for other uniparental shorebirds: white-rumped sandpiper *Calidris fuscicollis* 82% (Cartar & Montgomerie 1985), pectoral sandpiper *Calidris melanotos* 85% (Norton 1972) and 83%-87% (Kondratiev 1982), red phalarope *Phalaropus fulicaria* 70% (Erckmann 1981 cited in Cartar & Montgomerie 1985) or 85%-88% (Kondratiev 1982), red-necked phalarope *Phalaropus lobatus* 78% (Erckmann 1981 cited in Cartar & Montgomerie 1985) or 83%-94% (Kondratiev 1982), sanderling *Calidris alba* 81% (Parmelee 1970), Subantarctic snipe *Coenocorypha aucklandica* 71% (Miskelly 1989), common snipe *Gallinago gallinago* 78% (Green et al. 1990), ruff *Philomachus pugnax* 83%-89% (Kondratiev 1982), Temminck's stint *Calidris temminckii* 88%-92% (Kondratiev 1982) and great snipe *Gallinago media* 90% (Løfaldli 1985). Based on visual records the uniparental mountain plover's *Charadrius montanus* daytime attendance was 42% to 58% (Graul 1975), but daytime attendance in shorebirds is often lower than their overall attendance (Norton 1972; Cartar & Montgomerie 1985; Løfaldli 1985; Kálás 1986; Green et al. 1990; Pulliainen & Saari 1994) and visual records might underestimate attendance if birds were disturbed.

Biparental dotterel's nest attendance was between 91% and 96% (Kálás 1986; Pulliainen & Saari 1997), at the lower end of the values recorded for other biparental shorebirds:

Subantarctic snipe *Coenocorypha aucklandica* 100% (Miskelly 1989), dunlin *Calidris alpina* 98% (Norton 1972) or 92%-99% (Kondratiev 1982), Baird's sandpiper *Calidris bairdii* 96% (Norton 1972, some nests may have been uniparental, Norton pers. comm.), semipalmated sandpiper *Calidris pusilla* 100% (Cresswell et al. In press) and 93%-96% (Kondratiev 1982), golden plover *Pluvialis apricaria* 100% (Semenov-Tyan-Shanskii & Bragin 1969) and 97%-99% (Kondratiev 1982), grey plover *Pluvialis squatarola* 94%-97% (Kondratiev 1982), ringed plover *Charadrius hiaticula* 93%-95% (Kondratiev 1982), ruddy turnstone *Arenaria interpres* 90%-98% (Kondratiev 1982), spoon-billed sandpiper *Eurynorhynchus pygmeus* 88%-94% (Kondratiev 1982), rock sandpiper *Calidris ptilocnemis* 95% (Kondratiev 1982) and bar-tailed godwit *Limosa lapponica* 93% (Kondratiev 1982).

Løfaldli (1985) suggests that great snipe may have high nest attendance for a uniparental shorebird as their clutch mass is small relative to their body mass. Løfaldli (1985) also suggests that, although dotterel also have a small clutch mass relative to their body mass, they do not have higher nest attendance like great snipe because their three egg clutch is relatively more energetically expensive to incubate compared with the four egg clutch more typical of high latitudes. Assuming that Løfaldli's relationship between relative clutch mass and nest attendance applies generally (no data were presented), dotterel may depart from the relationship for other reasons such as phylogeny (dotterel are in the family Charadriidae while all the other uniparental shorebirds for which attendance data are given here are members of the family Scolopacidae), body stores, or the severity of energetic constraint experienced (uniparental dotterel's attendance appeared to vary between studies, possibly in relation to the degree of energetic constraint experienced: attendance values from a single study may provide a poor estimate for a species).

Drent et al.'s (1985) review of passerine nest attendance described a pattern of nest attendance with parental care similar to that of shorebirds:  $69 \pm 3\%$  for unprovisioned uniparental incubators,  $70 \pm 8\%$  for uniparental incubators fed by their mates and  $97 \pm 2\%$  for biparental care. In contrast, uniparental geese achieve nest attendance of more than 90% by partly or entirely fuelling their incubation period using stored body reserves (Thompson &

Raveling 1987; Reed et al. 1995). This ability to rely on body reserves is a consequence of geese's large body size (Moreno 1989b). Within geese, larger species may rely more heavily on stored reserves and achieve higher nest attendance than smaller species, although this may be, in part, because larger geese tend to migrate shorter distances and breed at lower latitudes, resulting in lower mass specific metabolic rates and less depleted body reserves (Reed et al. 1995).

*Why is attendance at biparental dotterel nests not higher?*

Cartar & Montgomerie (1985) suggest that biparental shorebirds should be able to achieve 100% nest attendance, except for disturbances due to predators and that any other time when the nest is unattended may be when eggs do not suffer any 'biologically significant cooling'. This seems to be the case in biparental dotterel, whose eggs spent only 2% of their time below 20°C although their nest attendance was only 94% in this study.

The majority of the 6% of time that biparental nests were unattended was not due to disturbance and on-duty parents were observed to make feeding trips similar to those of single parents (pers. obs.). The distinct pattern of biparental attendance in dotterel suggests a schedule of 'planned' trips, not precipitated by predator disturbance, as it seems unlikely that there should be any sufficiently regular pattern of disturbance by predators to drive such a pattern, especially as the predator assemblages varied between the two study sites. As uniparental nests shared a similar pattern of nocturnal nest attendance these dips in attendance of biparental nests were also unlikely to represent parental changeovers.

Why did biparental dotterel not increase their levels of nest attendance to the near total attendance achieved by some other biparental shorebird species? The 6% non-attendance of biparental nests appears to have little negative impact on the embryos' thermal environment. Since some of the shorebird species that have complete nest attendance breed in habitats where their unattended eggs are likely to cool more slowly than dotterel's, their extra nest attendance is probably having little effect on the amount of time the eggs spend below a

suitable temperature for development. This suggests that there are advantages to very high nest attendance and that either these advantages do not apply to dotterel or that biparental dotterel are constrained from achieving higher nest attendance.

In mild microclimates, the very high levels of nest attendance, beyond that necessary to maintain the embryonic thermal environment, may serve to reduce the risk of egg-predation (Kleindorfer & Hoi 1997). High nest attendance or the associated lower rate of trips to and from the nest may reduce the vulnerability of the nest to predation either because an attended nest is less conspicuous than an unattended nest (Storaas & Wegge 1997), because sitting parents can repel potential predators (e.g. Drent 1970; Harvey 1971; Inglis 1977) or because there is less parental activity around the nest for predators to detect (Drent 1970; Erikstad et al. 1982; Wiebe & Martin 1997; Martin & Ghalambor 1999).

The intensity of shorebirds' active nest defence probably increases with their size (Larsen 1993), so that high nest attendance may principally carry anti-nest predation benefits for larger shorebird species. Dotterel do carry out active nest defence, in the form of distraction displays (Cramp & Simmons 1983), but there is some suggestion that nests were less likely to be depredated if parents absented themselves when predators approached (Byrkjedal 1987), suggesting that a sitting parent may not reduce the risk of nest-predation, so that dotterel should only attend the nest as much as is necessary to maintain the embryos' thermal environment. However, this is not a very compelling explanation for why biparental dotterel do not achieve 100% attendance as, even if a nest is at less risk of predation if the parent is absent, more frequent journeys to and from the nest may attract the attention of predators that hunt by sight (although this would probably only apply to the  $64\% \pm 10\%$  of biparental trips made during daylight).

There is little information on the contribution of the sexes to biparental dotterel nests (Pulliainen & Saari 1997) and a possible alternative explanation for dotterel's relatively low biparental nest attendance is that an unequal contribution of the sexes to incubation or very long incubation shifts mean that the on-duty bird must make feeding trips to refuel during their



shift (although other biparental shorebird species have long incubation shifts, uninterrupted by feeding Kondratiev 1982; Cresswell et al. in press; D.P. Whitfield pers. comm.)

#### *Temporal and spatial variation in the degree of energetic constraint*

One of the recurrent themes of this study is how the factors that determine the degree of energetic constraint dotterel experience during incubation vary through space and time (as in Hohman 1986; Jones 1987; Pulliainen & Saari 1994). For example, in Scotland, climatic severity increases with altitude and to the north-west. As the two principal sites in this study were relatively low lying (the mean nest altitudes during 1997 and 1998 were: site B, 869m  $\pm$  22m a.s.l.; site D, 926m  $\pm$  12m) and southerly compared to the other main Scottish breeding areas, it is likely that the dotterel in this study would typically experience lower energetic costs of incubation and thermoregulation than most dotterel breeding in Scotland and they rarely experienced prolonged snow lie (D.P. Whitfield unpublished data). However, there may be more subtle geographic and temporal variation in the degree of energetic constraint experienced (e.g. Hepp et al. 1990). For example, the abundance of the favoured prey *Tipula montana* varied between and within sites (D.P. Whitfield unpublished data) and other prey items varied in abundance and availability between plant communities (Galbraith et al. 1993). Local topography influences the amount of rain and snow received, wind speed varies from large to very local spatial levels and different predator assemblages may impose different constraints on incubation scheduling (Pulliainen & Saari 1994).

The two years when incubation scheduling was studied were particularly cool and wet although there were no significant snowfalls while dotterel incubated. We were, therefore, able to investigate how incubation scheduling varied under conditions that excluded the extremes of high temperatures and snow lie. While this facilitated testing simpler hypotheses, it also means that we cannot supply a complete description of how incubation scheduling varies over the full range of conditions that nesting dotterel experience.

### *Energy saving behaviours in dotterel*

If energetic constraints during the incubation period limit LRS, individuals whose behaviours reduce energetic costs will have greater fitness. We found several energy saving behaviours in dotterel. Uniparental dotterel scheduled their feeding trips to coincide with weather conditions in which eggs would cool more slowly if unattended, reducing the energetic costs of egg-rewarming (although the less energetically constrained biparental dotterel did not).

Dotterel constructed nests that may have reduced their energetic cost of incubation. White & Kinney (1974) suggest that biparental incubators may have simple and, presumably, poorly insulated nests whereas uniparental incubators may have more complex nest structures. Complex, well insulated nests may reduce the costs of incubation and possibly thermoregulation for uniparental incubators. Dotterel and other uniparental shorebirds probably do not conform to this pattern as their nests generally consist of simple scrapes with linings composed of loose fragments of materials and dotterel's nests are probably less well lined than those of the biparental golden plover *Pluvialis apricaria* with which they share their breeding habitat (pers. obs.). Nest complexity varies between phylogenetic groups (Hansell 1984) and, as not all species within the group or even individuals within a species may share the same parental care system, some uniparental species within principally biparental groups may have simple, poorly insulated nests.

As well as phylogenetic limitations, there may also be environmental limitations on nest complexity: for example, some habitats, such as the high altitude or high latitude dwarfed plant communities that many shorebirds breed in, may be less amenable to the building of complex nests (although passerines such as the buntings *Plectrophenax nivalis* and *Calcarius lapponicus* that breed in the arctic can build complex nests in dwarfed plant communities, Cramp & Perrins 1994). Within their environmental and phylogenetic limitations, dotterel did appear to select nest sites that would reduce rates of heat loss and, consequently, reduce their energetic costs of incubation and thermoregulation. Dotterel selected nest sites where they could build deeper nest scrapes, which would accommodate larger nest linings and, possibly, more of the parent's body. There was some evidence that larger nest cups allowed

dotterel to spend more time incubating, which should have decreased the incubation period, possibly increasing hatching success and decreasing the depletion of body reserves: the energy saving of a good nest site may lessen the constraint of the energetic costs of incubation on LRS.

The choice of nest site may have to compromise several requirements (Götmark et al. 1995). Although the energetic costs of incubation and thermoregulation increased with wind speed, dotterel did not select nest sites that reduced their exposure to wind, perhaps because this would have compromised their view of predators. Nest sites that are advantageous under some weather conditions may be disadvantageous under others. For example, Costa's hummingbirds *Calypte costae* nesting in a hot microclimate were able to achieve high nest attendance but full sun in the hottest part of the day could have killed embryos during very short trips (Vleck 1981). Although dotterel occasionally experienced higher ambient temperatures and levels of solar heating that made them pant or shade their eggs (D.P. Whitfield unpublished data, pers. obs., although not during the two cool years of this study), choosing a nest site to enhance cooling on hot days was probably much less important than choosing a nest site that reduced cooling on the great majority of days when temperatures were below their lower critical temperature (Kersten & Piersma 1986).

Incubating birds may be able to conserve energy expended on thermoregulation through their orientation and posture (Cartar & Montgomerie 1985; Wiersma 1991). It is well documented that non-breeding shorebirds may orient themselves frontwards into the wind (e.g. Wiersma 1991). It is probably very important for minimising heat loss that the covering of the feathers that traps air and reduces convective cooling is not disrupted (Walsberg 1986; Wiersma 1991). At high wind speeds, orienting into the wind may also reduce wind resistance and so reduce the probability of being moved or pushed over by the wind. Sitting dotterel oriented forward into the wind and this probably gave the same kind of thermostatic benefits that non-incubating birds receive.

In cold, windy and wet weather dotterel also altered their posture, principally by drawing their head into their body and flattening themselves, as do other charadriiformes (Baerends et al. 1970; Drent et al. 1970; Cartar & Montgomerie 1985). Dotterel shook raindrops off their plumage (Pulliainen & Saari 1994; pers. obs). Like other shorebirds (Kondratiev 1982), while incubating in poor weather, dotterel reduced their frequency of activities such as preening, nest building and changing their position on the nest (pers. obs.): mallards *Anas platyrhynchos* reduced their rate of resettling on the nest at lower temperatures and during rain (Caldwell & Cornwell 1975).

Dotterel may also use more subtle behavioural and physiological mechanisms for reducing heat loss, such as ptiloerection, covering poorly insulated areas such as the carpal joints with contour feathers, peripheral vasoconstriction and countercurrent heat exchange in the legs and respiratory system (Calder & King 1974; Wiersma 1991; Wiersma et al. 1993). It may only be such energy saving behavioural mechanisms that keep shorebirds below the maximum sustainable ceiling of energy expenditure in cold conditions and allow them to winter in temperate climates (Wiersma et al. 1993).

As well as saving energy during incubation through scheduling, nest site selection, nest construction and orientation into the wind, dotterel probably also saved energy on nest defence when it was colder, by reducing their flushing distance to a perceived predator which would reduce the probable energetic cost of egg-rewarming.

#### *Daily energy expenditure and compensation*

The energetic cost of thermoregulation decreases with increasing temperature (Rintamäki et al. 1983; Obst et al. 1987; Webster & Weathers 1988; Wiersma & Piersma 1994), decreasing wind speed (Goldstein 1983 & review therein; Walsberg 1986; Webster & Weathers 1988; Williams & Dwinell 1990; Bakken & Lee 1992; Wiersma & Piersma 1994; Wolf & Walsberg 1996) and an increasing intensity of solar radiation (De Jong 1976 & references therein; Wiersma & Piersma 1994; Wolf & Walsberg 1996), although the costs of thermoregulation increase above the upper critical temperature, which most frequently occurs under intense

solar radiation, (e.g. De Jong 1976). However, Bryant & Tatner's (1991) meta-analysis of intraspecific variation in avian energy expenditure found no consistent effects of temperature, wind speed or insolation on DEE (although all three significantly affected expenditure within at least one species in the analysis). The lack of any consistent effect may result in part from compensatory behaviours: dotterel, for example, altered their incubation scheduling as weather conditions worsened, so that less energy was expended on incubation, potentially masking the effects of weather variables on thermoregulation.

Alternatively, it could be that variation in energetic costs other than thermoregulation swamps the variation in DEE due to the effect of weather conditions on the cost of thermoregulation, although BMR plus thermoregulation typically make up 40-60% of a bird's energy expenditure (Bakken 1990). However, in species that spend much time in energetically expensive activities, such as the aerial foragers that made up over half the species in Bryant & Tatner's study (1991), much of the potential cost of thermoregulation may be accounted for by metabolic substitution, so that thermoregulation becomes a relatively minor energetic cost. None of the species in this meta-analysis inhabited an environment where thermoregulation might be expected to be as important a component of the energy budget as in dotterel. Wind, insolation and temperature are important influences on the costs of thermoregulation and overall field metabolic rate in shorebirds that winter in the temperate zone or breed in the arctic (Wiersma 1991; Wiersma & Piersma 1994; Piersma & Morrison 1994). An incubating shorebird may have little scope for varying its cost of thermoregulation and dotterel appeared to compensate for a high cost of thermoregulation by decreasing their investment of time and energy in incubation. Such compensatory changes in behaviour may mask variation in thermostatic costs on DEE.

### **The life history theory implications of energetic constraint during incubation**

Life-history theory predicts that animals maximise their lifetime reproductive success by balancing their investment in a current breeding attempt against any consequent reductions in their survival or future productivity. I discuss whether dotterel's investment in reproduction, in

terms of their clutch size and their expenditure of time and energy on incubation, is limited by energetic constraint. Life-history theory also predicts that older individuals that have lower residual reproductive success should invest more heavily in reproduction. I discuss whether we should predict greater investment in reproduction by older dotterel.

*Is dotterel's clutch size limited by energetic constraint during the incubation period?*

An important component of an animal's lifetime reproductive success is the number of young it produces per breeding attempt (Oring et al. 1991). Dotterel's clutch size is usually three and very rarely four, smaller than the clutch size of most other fully precocial shorebirds that breed in the temperate and arctic zones. The energetic cost of incubation may increase with clutch size (Biebach 1981; Biebach 1984; Haftorn & Reinertsen 1985; Moreno & Sanz 1994) and Kálás & Løfaldli (1987) suggest that dotterel's clutch size is limited to three by energetic constraint during the incubation period. Incubation capacity may limit many other shorebirds to four egg clutches (Hills 1980). Experiments such as Kálás & Løfaldli's (1987) and Hill's (1980) that increase clutch size above the natural maximum may have limited validity if a species has subsequently evolved adaptations (such as brood patch configuration) to a determinant clutch size that may initially have been limited by incubation ability. However, three eggs is the most common clutch size across *Charadrius* species, which breed in a wide range of habitats and have different parental care systems and so, probably, experience very different degrees of energetic constraint (Table 1).

The number of offspring a male dotterel can produce from each brood may also be limited, not by his ability to care for them, but by the female's ability to produce more eggs. In dotterel it is tempting to suggest that, because females may be polyandrous, with up to five mates per season (Holt et al. 2002) that they will limit investment in any one clutch to allow investment in future breeding attempts (Johnsgard 1973; Milonoff 1991; review of costs of egg production in Monaghan & Nager 1997). However, dotterel's closest relations also have typically have three egg clutches but socially monogamous mating systems and biparental care (Table 1).

Table 1. Clutches sizes, breeding systems and breeding habitat of the genus *Charadrius* (all taken from del Hoyo et al. 1996).

Species	modal clutch size	incubation parental care	mating system	breeding habitat	lowest breeding latitude	highest breeding latitude
<i>C. obscurus</i>	3	biparental	monogamous	exposed hill tops >300m a.s.l.	34	47
<i>C. hiaticula</i>	4	biparental	monogamous	beaches	49	85
<i>C. semipalmatus</i>	3-4	biparental	monogamous	beaches & plains	43	73
<i>C. placidus</i>	4?	?	?	beaches	32	52
<i>C. dubius</i>	4	biparental	monogamous/ polyandrous	beaches	3	69
<i>C. wilsonia</i>	3	biparental	monogamous	beaches	0	41
<i>C. vociferous</i>	4	biparental/uniparental?	monogamous (occasionally double brooded)	grassland, agricultural and disturbed land	3	65
<i>C. melodus</i>	4	biparental	monogamous	beach	33	58
<i>C. thoracicus</i>	2?	?	?	lowland	12	24
<i>C. pecuarius</i>	2	biparental	monogamous	beaches	0	35
<i>C. santaehelenae</i>	1-2	?	?	upland	15	16
<i>C. tricoloris</i>	2	biparental	monogamous	beaches	0	35
<i>C. forbesi</i>	2-3	biparental	monogamous	upland	0	13
<i>C. marginatus</i>	2	biparental	monogamous	beaches	0	35
<i>C. alexandrinus</i>	3	biparental	monogamous	beaches	4	57
<i>C. javanicus</i>	?	?	?	coastal lowland	6	9
<i>C. ruficapillus</i>	2	biparental	?	beaches	10	43
<i>C. peronii</i>	3	?	?	beaches	0	19
<i>C. pallidus</i>	2	biparental/uniparental?	monogamous/ double brooded?	beaches	2	35
<i>C. collaris</i>	2	?	?	beaches & savannas	0	47
<i>C. alticola</i>	?	?	?	puna zone of high mountains	7	27
<i>C. falklandicus</i>	3	?	?	beaches & savannas	32	56
<i>C. bicinctus</i>	3	biparental/uniparental?	monogamous/ occasionally double brooded	beaches, montane, upland, lowland	34	51
<i>C. mongolus</i>	3	biparental	monogamous	montane, dunes & shingle	34	68
<i>C. leshenaultii</i>	3	biparental	monogamous	desert & semi-desert	32	53
<i>C. asiaticus</i>	3	biparental	monogamous	desert & steppe	35	60
<i>C. veredus</i>	?	?	?	beaches	40	52
<i>C. morinellus</i>	3	uniparental & occasionally biparental	monogamous, polyandrous, polygynous	montane & tundra	42	76
<i>C. modestus</i>	2	biparental	monogamous?	lowland grassland to 2000m foothills	36	56
<i>C. montanus</i>	3	uniparental	monogamous including double clutching, polyandrous, polygynous	prairie	39	53
<i>C. rubricollis</i>	2-3	biparental	monogamous	dunes & beaches	31	43
<i>C. novaeseelandiae</i>	3	biparental	monogamous	beaches & inland salt meadows	44	44

Analogous to the need to be able to lay numerous clutches in polyandrous species, high rates of egg predation, irrespective of the pattern of parental care, may select for a small clutch sizes to allow replacement clutches to be laid (Milonoff 1991) although other studies suggest that only intense predation pressure may influence clutch size e.g. (Lundberg 1985; Martin 1988): for example, biparental and socially monogamous ringed plovers *Charadrius hiaticula* (with a clutch size of four) that suffered high rates of egg-predation laid up to five clutches in a season (Pienkowski 1984).

The three principal phases of reproduction that might place energetic constraints on clutch size are egg production, incubation and brood care. Neither egg production nor incubation could be dismissed as the potentially limiting stage. Could brood care have been the limiting stage? Dotterel's chicks are self-feeding so brood care would be most likely to limit brood size through brooding capacity. In a cool environment, brooding may occupy a large proportion of the parent's time, especially when the chicks are young and least endothermic (Beintema & Visser 1989; Visser & Ricklefs 1993b; D.P. Whitfield unpublished data).

The experimental and circumstantial evidence that dotterel's clutch size is limited by energetic constraint during the incubation period is weak, but the reduction in nest attendance with increasing energetic costs (with a consequent increase in the incubation period and a possible reduction in hatching success), the incidence of egg neglect, non-adaptive mass loss and the decline in nest attendance with smaller body reserves all suggest that dotterel experienced energetic constraint during incubation that may ultimately limit LRS.

#### *Allocation of resources between care of eggs and self*

Dotterel did not schedule their incubation to a pattern that would ensure the eggs were always at a temperature suitable for development. This was interpreted to be a consequence of parents operating under energetic constraint, either to balance their energy budgets or because they were at their maximum sustainable metabolic rate or maximal thermogenesis, so that they could not fuel such a schedule. This parallels the idea that birds that are feeding young fly at a speed that minimises their energy expenditure rather than maximising the



delivery rate of food because they are under energetic constraint (reviewed in Cuthill & Houston 1997). Parents caring for either eggs or chicks may experience energetic constraint, which means that they limit their allocation of time or energy to the care of their young. Birds' level of energetic expenditure on reproduction may attempt to maximise LRS: increases in the success of the current breeding attempt through increased energetic investment must be traded-off against any concomitant decreases in parental survival and future productivity (Bryant 1988; Bryant & Tatner 1991; Erikstad et al. 1998).

A breeding bird suffering energetic constraint can either reduce investment in its young or reduce its own body reserves (Ricklefs 1974; Westerterp & Bryant 1984). Dotterel appeared to vary both investment in incubation and use of their body reserves, depending on the degree of constraint. When weather conditions worsened from good to moderate dotterel appeared to increase their energetic investment in incubation but when weather conditions further deteriorated they reduced expenditure on incubation. Dotterel also appeared to increase their energetic expenditure on nest defence when their energetic costs were lower in better weather and when food was more abundant. However, dotterel did not increase their energetic investment in incubation when food was more abundant or when sharing incubation duties. Instead, they appeared to channel 'spare' energy into body reserves.

### *Parental age*

Incubation and nest defence constitute parental investment. In some of our analyses we tested whether age affects measures of fitness or parental investment. Life-history theory provides the hypothesis that, in species in which residual reproductive value declines with age, individuals should increase parental investment as they become older (Carlisle 1982). Assuming a finite maximum lifespan, residual reproductive value will decline with age (Pianka & Parker 1975) but the pattern of change in residual reproductive value with age depends on the extent of senescent decline (Newton 1989). In addition, if average mortality is high and senescent decline only occurs at great age or if a large proportion of deaths are stochastic events independent of an individual's quality or condition, this will dampen any effect of

senescence or finite life-span on residual reproductive value. However, in the absence of good data on age-specific mortality for dotterel, we cannot reasonably predict any pattern of variation in residual reproductive value with age. Indeed, there may be no clear general pattern of mortality with age in shorebirds (Soikkeli 1967; Hildén 1977; Goss-Custard et al. 1982; Peach et al. 1994; Insley et al. 1997) but the sampling methods used in these studies might not, anyway, detect increased mortality in old age (Botkin & Miller 1974; Hildén 1977; Newton 1989).

Even in species whose residual reproductive value decreases strongly with age, the effects on parental investment may be confounded: senescence may reduce breeding performance and so apparent parental investment (Carlisle 1982), or phenotypic changes with age may allow a parent to increase parental investment without greater reduction in residual reproductive output (Partridge 1989). In cross-sectional studies of changes with age, differences in the longevity of different phenotypes may obscure the true variation (Clutton-Brock 1988). The longitudinal analyses in this study (comparing the same individual at different ages) avoid this problem (Clutton-Brock 1988).

We found no significant effect of a dotterel's age on either nest defence or body reserves. In both analyses we looked at variation within individuals, to attempt to control for as many other potentially confounding effects as possible. However this meant that our sample sizes were limited to 12 and 17 individuals in the body reserve and nest defence analyses, respectively, and probably more importantly the median age difference within individuals in the samples of 1.5 and three years may have been too small to give much variation in residual reproductive output or senescence. In summary, in the absence of knowledge of the pattern of mortality with age in dotterel, we cannot frame clear hypotheses of how parental investment should vary with age and our samples were anyway probably inadequate to test these hypotheses with sufficient statistical power.

## **The Implications of energetic constraint during incubation for mating systems**

If energetic constraint during incubation means that uniparental nests are less successful than biparental nests then this will have consequences for parental care and mating systems.

In some species, an individual that seeks new mates must desert its current mate. This may most frequently be the case when the deserting sex is female because females must desert for at least the time it takes to produce a new clutch while a male may be able to mate with a new female in a very brief absence from his original mate. If polygamy requires mate desertion, for it to be a successful mating strategy, the individual must gain greater reproductive success through finding new mates than it will lose by leaving its deserted mate to care alone (Maynard Smith 1977; Székely & Cuthill 2000).

The benefits of mate desertion will depend on the operational sex ratio and breeding density as well as an individual's quality or attractiveness (Emlen & Oring 1977; Székely & Williams 1995). Mate desertion will carry costs for both members of the pair if uniparental care is less successful than biparental care. This is likely to occur if it is difficult for a single carer to manage its energy budget or time while providing sufficient brooding and food to the offspring or if two parents are better able to either prevent offspring predation or defend a territory against conspecifics (Larsen et al. 1996). For example, polygyny may often occur in birds that eat seeds or fruit because periods of high food availability mean that a single parent can successfully feed a brood (Krebs & Davies 1997). High energetic costs and low food availability or stored body reserves during the incubation period could then make polygyny an unsuccessful mating strategy. The ability of a parent to care alone while successfully managing its energy budget is a prerequisite for uniparental care and polygamy in some systems. Once mate desertion and uniparental care is established the selective pressure for the lone carer to reduce energetic costs will presumably increase.

Uniparental incubation is, perhaps, surprisingly common amongst sandpipers breeding in the arctic, given the high costs of thermoregulation and incubation associated with a cold climate (Cartar & Montgomerie 1985; Piersma & Morrison 1994; Whitfield & Tomkovich 1996;

Andreev 1999). Cartar & Montgomerie (1985) attribute the high incidence of uniparental care in this group to their mating systems. However, although mating and parental care systems are closely linked, the direction of causality may not be this clear (Whitfield & Tomkovich 1996; Reynolds & Székely 1997; Owens & Bennett 1997). The degree of energetic constraint a uniparental incubator experiences will depend on its energy intake as well as its expenditure of energy. High food availability may mean that arctic-alpine uniparental shorebirds are less energetically constrained than might be expected from their energy expenditure, but mass loss in uniparental shorebirds, which in dotterel at least is probably a consequence of energetic constraint, suggests that they do at least periodically experience energetic constraint (Soloviev & Tomkovich 1997; Hegyi & Sasvári 1998).

Uniparental dotterel were energetically constrained during incubation to the extent that they depleted their body reserves and reduced their investment in incubation, with deleterious consequences for hatching success. However, it might be expected that in the arctic, where most uniparental shorebirds breed (Whitfield & Tomkovich 1996), energetic demands will be even higher. These often small sandpipers, with a smaller capacity for the storage of body reserves to help fuel their higher mass-specific metabolic rates through incubation, often have female uniparental incubation, so that the parent also commences incubation with body reserves depleted by egg production (Cartar & Montgomerie 1985). How do these single parents manage their high energetic costs to successfully care for their eggs and themselves? Higher food availability could allow high energetic costs to be more easily borne or, alternatively, thermoregulation or incubation in Scotland's montane zone may not be less energetically costly than in colder regions. Dotterel's Scottish breeding habitat is characterised by high wind speeds and much precipitation. The effects of precipitation on the energetic costs of thermoregulation and incubation are little known but wind may greatly increase the costs of thermoregulation and incubation (Walsberg 1986; review in Bryant & Tatner 1991; Wiersma & Piersma 1994; Wolf & Walsberg 1996).

## **Conclusion**

This study adds to the growing evidence that, under certain ecological conditions and patterns of parental care, incubation can be a period of energetic constraint that may limit LRS (Yom-Tov & Hilborn 1981; Heaney & Monaghan 1996; Hainsworth et al. 1998; Bryan & Bryant 1999; Reid et al. 1999). However, it would be incorrect to try to reverse the general notion that it is chick-rearing rather than the incubation period that generally is the breeding energetic bottleneck that limits LRS. The relative degrees of constraint experienced at different stages will depend on many biotic and abiotic factors such as the thermal environment, food type and availability, mating and parental care systems and the pattern of development of the chicks (Williams 1996). Energy deficits may also be cumulative so that, even though a stage is not the most energetically constrained, it may use up some body reserves that cannot, then, be used at the more constrained stage (Heaney & Monaghan 1996).

Altricial species have often been used to support the idea that incubation is not an energetically constrained stage of breeding, although incubation has also been found to be relatively energetically inexpensive in some precocial species (Gabrielsen 1989). But even in a fully precocial species with self-feeding chicks such as the dotterel, where energetic constraint during the incubation period has been demonstrated, we cannot discount the idea that the parents are also energetically constrained while caring for chicks. Although parents do not expend energy collecting food for their self-feeding chicks, their care may still impose high costs in terms of time and energy. In a cold climate chicks may require much brooding (Visser & Ricklefs 1993a; Visser & Ricklefs 1993b; Visser 1998) and, as dotterel chicks often do not brood synchronously (D.P. Whitfield unpublished data), this may further reduce the time available for the parent to feed. The energetic cost of brooding chicks may also be relatively high since they are no longer in the favourable nest microclimate. In addition, much time is also occupied in vigilance for predators of the relatively slow-moving chicks (D.P. Whitfield unpublished data). The time and energy required to brood and defend the chicks decreases with their age as their self-thermoregulatory and locomotor abilities develop, so that, any energetic constraint parents experience will probably be most severe during the period following hatch.

The costs of egg production have also been forwarded as an energetically constrained stage of breeding that may limit LRS (Monaghan & Nager 1997). As most dotterel breeding attempts are cared for by the male alone, the principal energetic costs of reproduction that a female must bear are securing a mate and producing a clutch.

Regardless of whether the energetic costs of egg production and/or chick rearing are high in dotterel, the energetic costs of incubation appear to be important in the evolution of dotterel's behaviour. Dotterel exhibited a number of behaviours that allowed them to reduce their costs during the incubation period: dotterel capped their energetic expenditure on incubation and matched feeding trips to conditions that would reduce the cost of egg rewarming, they switched to a less costly anti-nest predation strategy when costs were higher and selected nest sites that allowed larger nests with bigger linings and they oriented into the wind while sitting on the nest. In summary, dotterel were energetically constrained during incubation and adopted behaviours that reduced their degree of energetic constraint.

## References

- Andreev,A.V. 1999. Energetics and survival of birds in extreme environments. Ostrich , 70, 13-22.
- Baerends,G.P., Drent,R.H., Glas,P. & Groenewold,H. 1970. An ethological analysis of incubation behaviour in the Herring Gull. Behaviour Supplement , 17, 135-234.
- Bakken,G.S. 1990. Estimating the effect of wind on avian metabolic rate with standard operative temperature. Auk , 107, 587-594.
- Bakken,G.S. & Lee,K.F. 1992. Effects of wind and illumination on behavior and metabolic-rate of American Goldfinches (*Carduelis tristis*). Auk , 109, 119-125.
- Beintema,A.J. & Visser,G.H. 1989. The effect of weather on time budgets and development of chicks of meadow birds. Ardea , 77, 181-192.
- Biebach,H. 1981. Energetic costs of incubation on different clutch sizes in Starlings. Ardea , 69, 141-142.

- Biebach, H. 1984. Effect of clutch size and time of day on the energy expenditure of incubating Starlings (*Sturnus vulgaris*). Physiological Zoology , 57, 26-31.
- Botkin, D.B. & Miller, R.S. 1974. Mortality rates and survival of birds. American Naturalist , 108, 181-192.
- Bryan, S.M. & Bryant, D.M. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in Great Tits, *Parus major*. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 266, 157-162.
- Bryant, D.M. 1988. Energy expenditure and body mass changes as measures of reproductive cost in birds. Functional Ecology , 2, 23-34.
- Bryant, D.M. & Tatner, P. 1991. Intraspecific variation in avian energy expenditure: correlates and constraints. Ibis , 133, 236-245.
- Byrkjedal, I. 1987. Antipredator behaviour and breeding success in Greater Golden Plover and Eurasian Dotterel. The Condor , 89, 40-47.
- Calder, W.A. & King, J.R. 1974. Thermal and caloric relations of birds. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 259-413. New York: Academic Press.
- Caldwell, P.J. & Cornwell, G.W. 1975. Incubation behaviour and temperatures of the Mallard duck. Auk , 92, 706-731.
- Carlisle, T.R. 1982. Brood success in variable environments: implications for parental care allocations. Animal Behaviour , 30, 824-836.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour , 95, 261-289.
- Cartar, R.V. & Montgomerie, R.D. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. The Condor , 89, 252-260.
- Clutton-Brock, T.H. 1988. Introduction. In: Reproductive success: studies of individual variation in contrasting breeding systems (Ed. by T.H. Clutton-Brock), pp. 1-10. Chicago: University of Chicago.
- Cramp, S. & Perrins, C.M. 1994. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume IX: Buntings and New World Warblers. Oxford: Oxford University Press.

- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Cresswell, W., Holt, S., Whitfield, D.P., Reid, J.B. & Mellanby, R. In press. The effects of steady state incubation costs on incubation scheduling in semipalmated sandpipers  
Behavioural Ecology
- Croxall, J.P. 1982. Energy cost of incubation and moult in petrels and penguins. Journal of Animal Ecology , 51, 177-194.
- Croxall, J.P. & Ricketts, C. 1983. Energy costs of incubation in the Wandering Albatross *Diomedea exulans*. Ibis , 125, 33-39.
- Cuthill, I.C. & Houston, A.I. 1997. Managing time and energy. In: Behavioural ecology: an evolutionary approach (Ed. by J.R. Krebs & N.B. Davies), pp. 97-120. Oxford: Blackwell Scientific.
- De Jong, A.A. 1976. The influence of simulated solar radiation on the metabolic rate of White-crowned Sparrows. The Condor , 78, 174-179.
- Drent, R.H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Supplement , 17, 1-132.
- Drent, R.H. & Daan, S. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea , 68, 225-252.
- Drent, R.H., Postuma, K.H. & Joustra, T. 1970. The effect of egg temperature on incubation behaviour in the Herring Gull. Behaviour Supplement , 17, 235-260.
- Drent, R.H., Tinbergen, J.M. & Biebach, H. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. Netherlands Journal of Zoology. 35, 103-123.
- Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. Science , 197, 215-223.
- Eppley, Z.A. 1996. Charadriiform birds in Antarctica - behavioral, morphological, and physiological adjustments conserving reproductive success. Physiological Zoology , 69, 1502-1554.



- Erckmann, W.J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. In: Social Behaviour of Female Vertebrates (Ed. by S.K.Wasser), pp. 113-168. London: Academic press.
- Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. 1998. On the cost of reproduction in long-lived birds: The influence of environmental variability. Ecology, 79, 1781-1788.
- Erikstad, K.E., Myrberget, S. & Blom, R. 1982. Territorial crows as predators on Willow Ptarmigan nests. Journal of Wildlife Management, 46, 109-114.
- Erikstad, K.E. & Tveraa, T. 1995. Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*. Oecologia, 103, 270-274.
- Gabrielsen, G.W. 1989. Energy saving in incubating birds. In: Physiology of cold adaptation in birds (Ed. by C.Bech & R.E.Reinertsen), pp. 325-328. New York: Plenum Press.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D.P. & Thompson, D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. Ibis, 135, 148-155.
- Goldstein, D.L. 1983. Effect of wind on avian metabolic rate with particular reference to Gambel's Quail. Physiological Zoology, 56, 493-505.
- Goss-Custard, J.D., Le V.Dit Durrell, S.E.A., Sitters, H.P. & Swinfen, R. 1982. Age-structure and survival of a wintering population of Oystercatchers. Bird Study, 29, 83-98.
- Götmark, F., Blomqvist, D., Johansson, O.C. & Bergkvist, J. 1995. Nest-site selection - a trade-off between concealment and view of the surroundings. Journal of Avian Biology, 26, 305-312.
- Graul, W.D. 1975. Breeding biology of the Mountain Plover. Wilson Bulletin, 87, 6-31.
- Green, R.E., Hirons, G.J.M. & Cresswell, B.H. 1990. Foraging habitats of female Common Snipe *Gallinago gallinago* during the incubation period. Journal of Applied Ecology, 27, 325-335.
- Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. Omis Scandinavica, 19, 97-110.
- Haftorn, S. & Reinertsen, R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free-living Blue Tit. Auk, 102, 470-478.

- Hainsworth, F.R., Moonan, T., Voss, M.A., Sullivan, K.A. & Weathers, W.W. 1998. Time and heat allocations to balance conflicting demands during intermittent incubation by Yellow-eyed Juncos. Journal of Avian Biology , 29, 113-120.
- Hansell, M.H. 1984. Animal architecture and building behaviour. Harlow, UK: Longman.
- Harris, H.J. 1970. Evidence of stress response in breeding Blue-winged Teal. Journal of Wildlife Management , 34, 747-755.
- Harvey, J.M. 1971. Factors affecting Blue Goose nesting success. Canadian Journal of Zoology , 49, 223-234.
- Heaney, V. & Monaghan, P. 1996. Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 263, 1719-1724.
- Hegyí, Z. & Sasvári, L. 1998. Parental condition and breeding effort in waders. Journal of Animal Ecology , 67, 41-53.
- Hepp, G.R., Kennamer, R.A. & Harvey, W.F. 1990. Incubation as a reproductive cost in Wood Ducks. Auk , 107, 756-764.
- Hildén, O. 1977. Population dynamics in Temminck's stint *Calidris temminckii*. Oikos , 30, 17-28.
- Hills, S. 1980. Incubation capacity as a limiting factor of shorebird clutch size. American Zoologist , 20, 774
- Hohman, W.L. 1986. Incubation rhythms of Ring-necked Ducks. The Condor , 88, 290-296.
- Holt, S., Whitfield, D.P. & Gordon, J. 2002. Potential reproductive rates in the Eurasian dotterel *Charadrius morinellus*. Bird Study , 49, 87-88
- Inglis, I.R. 1977. The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. Animal Behaviour , 25, 747-764.
- Insley, H., Peach, W.J., Swann, B. & Etheridge, B. 1997. Survival rates of Redshank *Tringa totanus* wintering on the Moray Firth. Bird Study , 44, 277-289.
- Johnsgard, P.A. 1973. Proximate and ultimate determinants of clutch size in Anatidae. Wildfowl , 24, 144-149.

- Jones,G. 1987. Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. Journal of Animal Ecology , 56, 229-245.
- Kálás,J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Kálás,J.A. & Løfaldli,L. 1987. Clutch size in the Dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? Ornis Scandinavica , 18, 316-319.
- Kendeigh,S.C. 1963. Thermodynamics of incubation in the house wren, *Troglodytes aedon*. In: Proceedings of the XIII International Ornithological Congress pp. 884-904.
- Kersten,M. & Piersma,T. 1986. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. Ardea , 75, 175-188.
- Kleindorfer,S. & Hoi,H. 1997. Nest predation avoidance: an alternative explanation for male incubation in *Acrocephalus melanopogon*. Ethology , 103, 619-631.
- Kondratiev,A.J. 1982. Biology of waders in the tundras of the north-east of Asia. Academy of Sciences of the USSR: Nauka, Moskow
- Krebs,J.R. & Davies,N.B. 1997. The evolution of behavioural ecology. In: Behavioural ecology: an evolutionary approach (Ed. by J.R.Krebs & N.B.Davies), pp. 3-12. Oxford: Blackwell Science.
- Larsen,T. 1993. On the causes of aggressive nest defence in waders and some of its implications on their breeding biology. PhD thesis, University of Bergen.
- Larsen,T., Sordahl,T.A. & Byrkjedal,I. 1996. Factors related to aggressive nest protection behaviour: A comparative study of Holarctic waders. Biological Journal of the Linnean Society , 58, 409-439.
- Løfaldli,L. 1985. Incubation rhythms in the Great Snipe *Gallinago media*. Holarctic Ecology , 8, 107-112.
- Lundberg,S. 1985. The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. Oikos , 45, 110-117.
- Lyon,B.E. & Montgomerie,R.D. 1987. Ecological correlates of incubation feeding: A comparative study of high arctic finches. Ecology , 68, 713-722.

- Martin, T.E. 1988. Nest placement: implications for selected life-history traits, with special reference to clutch size. American Naturalist , 132, 900-910.
- Martin, T.E. & Ghalambor, C.K. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? American Naturalist , 153, 131-139.
- Maynard Smith, J. 1977. Parental investment: a prospective analysis. Animal Behaviour , 25, 1-9.
- Mertens, J.A.L. 1977. The energy requirements for incubation in Great Tits, *Parus major* L. Ardea , 65, 184-196.
- Milonoff, M. 1991. Renesting ability and clutch size in precocial birds. Oikos , 62, 189-194.
- Miskelly, C.M. 1989. Flexible incubation system and prolonged incubation in New Zealand Snipe. Wilson Bulletin , 101, 127-132.
- Monaghan, P. & Nager, R.G. 1997. Why don't birds lay more eggs? Trends In Ecology & Evolution , 12, 270-274.
- Moreno, J. 1989a. Energetic constraints on uniparental incubation in the wheatear *Oenanthe oenanthe*. Ardea , 77, 107-115.
- Moreno, J. 1989b. Strategies of mass change in breeding birds. Biological Journal of the Linnean Society , 37, 297-310.
- Moreno, J. & Sanz, J.J. 1994. The relationship between the energy-expenditure during incubation and clutch size in the Pied Flycatcher *Ficedula hypoleuca*. Journal of Avian Biology , 25, 125-130.
- Morton, M.L. & Pereyra, M.E. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). Auk , 102, 25-37.
- Newton, I. 1989. Synthesis. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 441-470. London: Academic Press.
- Norton, D.W. 1972. Incubation schedules of four species of Calidrine sandpipers at Barrow, Alaska. The Condor , 74, 164-176.
- Norton, D.W. 1973. Ecological energetics of Calidrine sandpipers breeding in northern Alaska. PhD thesis, University of Alaska, Fairbanks.
- Obst, B.S., Nagy, K.A. & Ricklefs, R.E. 1987. Energy utilization by Wilson's Storm-petrel. Physiological Zoology , 60, 200-210.

- Oring, L.W., Colwell, M.A. & Reed, J.M. 1991. Lifetime reproductive success in the Spotted Sandpiper (*Actitis macularia*): sex differences and variance components. Behavioural Ecology and Sociobiology , 28, 425-432.
- Owens, I.P.F. & Bennett, P.M. 1997. Variation in mating system among birds: ecological basis revealed by hierarchical comparative analysis of mate desertion. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 264, 1103-1110.
- Parmelee, D.F. 1970. Breeding behaviour of the sanderling in the Canadian high arctic. Living Bird , 9, 97-146.
- Partridge, L. 1989. Lifetime reproductive success and life-history evolution. In: Lifetime reproduction in birds (Ed. by I. Newton), pp. 421-440. London: Academic Press.
- Peach, W.J., Thompson, P.S. & Coulson, J.C. 1994. Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. Journal of Animal Ecology , 63, 60-70.
- Peterson, C.C., Nagy, K.A. & Diamond, J. 1990. Sustained metabolic scope. Proc. Natl. Acad. Sci. USA , 87, 2324-2328.
- Pianka, E.R. & Parker, W.S. 1975. Age-specific reproductive tactics. American Naturalist , 109, 453-464.
- Pienkowski, M.W. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. Journal of Zoology, London , 202, 83-114.
- Piersma, T. & Morrison, R.I.G. 1994. Energy expenditure and water turnover of incubating Ruddy Turnstones: high costs under high Arctic conditions. Auk , 111, 366-376.
- Pulliainen, E. & Saari, L. 1994. Incubation behaviour of the Dotterel *Charadrius morinellus*. Oecologia Montana , 3, 27-34.
- Pulliainen, E. & Saari, L. 1997. Attendance at the nest of polyandrous Dotterel *Charadrius morinellus* in Finland. Ardea , 85, 67-71.
- Reed, A., Hughes, R.J. & Gauthier, G. 1995. Incubation behaviour and body mass in Greater Snow Geese. The Condor , 97, 993-1001.
- Reid, J.M., Monaghan, P. & Ruxton, G.D. 1999. The effect of cooling rate on starling, *Sturnus vulgaris*, incubation strategy. Animal Behaviour , 58, 1161-1167.

- Reynolds, J.D. & Székely, T. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. Behavioral Ecology , 8, 126-134.
- Ricklefs, R.E. 1974. Energetics of reproduction in birds. In: Avian energetics (Ed. by R.A.J. Paynter), pp. 152-297. Nuttall Ornithological Club.
- Rintamäki, H., Saarela, S., Marjakangas, A. & Hissa, R. 1983. Summer and winter temperature regulation in the Black Grouse *Lyrurus tetrix*. Physiological Zoology , 56, 152-159.
- Semenov-Tyan-Shanskii, O.I. & Bragin, A.B. 1969. Incubation conditions for some precocial birds in the subarctic. Byulleten Moskovskogo Obshchestva Ispytatelei Prirody, Otdel. Biol. 74, 50-66.
- Smith, H.G., Källander, H., Hultman, J. & Sanzén, B. 1989. Female nutritional state affects the rate of male incubation feeding in the Pied Flycatcher *Ficedula hypoleuca*. Behavioural Ecology and Sociobiology , 24, 417-420.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Annales Zoologici Fennici , 4, 158-198.
- Soloviev, M.Y. & Tomkovich, P.S. 1997. Body mass changes in waders (Charadrii) in a high arctic area at Northern Taimyr, Siberia. Journal Fur Ornithologie , 139, 271-281.
- Storaas, T. & Wegge, P. 1997. Relationship between patterns of incubation and predation in sympatric Capercaillie *Tetrao urogallus* and Black Grouse *T. tetrix*. Wildlife Biology , 3, 163-167.
- Székely, T. & Cuthill, I.C. 2000. Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. Proceedings Of The Royal Society Of London Series B-Biological Sciences , 267, 2087-2092.
- Székely, T. & Williams, T.D. 1995. Costs and benefits of brood desertion in female Kentish Plovers, *Charadrius alexandrinus*. Behavioral Ecology And Sociobiology , 37, 155-161.
- Thompson, D.B.A. & Whitfield, D.P. 1993. Research Progress Report: Research on mountain birds and their habitats. Scottish Birds , 17, 1-8.
- Thompson, S.C. & Raveling, D.G. 1987. Incubation behaviour of Emperor Geese compared to other Geese: interactions of predation, body size and energetics. Auk , 104, 707-716.
- Thomson, D.L., Monaghan, P. & Furness, R.W. 1998. The demands of incubation and avian clutch size. Biological Review , 73, 293-304.

- Tombre, I.M. & Erikstad, K.E. 1996. An experimental study of incubation effort in high-Arctic Barnacle Geese. Journal of Animal Ecology , 65, 325-331.
- Tulp, H., Schekkerman, H., Piersma, T., Jukema, J., de Goeij, P., & van de Kam, J. 1998. Breeding waders at Cape Sterlegova, northern Taimyr, in 1994. Zeist, The Netherlands: WIWO
- Visser, G.H. 1998. Development of temperature regulation. In: Avian growth and development: evolution within the altricial-precocial spectrum (Ed. by J.M. Starck & R.E. Ricklefs), pp. 117-156. Oxford: Oxford University Press.
- Visser, G.H. & Ricklefs, R.E. 1993a. Development of temperature regulation in shorebirds. Physiological Zoology , 66, 771-792.
- Visser, G.H. & Ricklefs, R.E. 1993b. Temperature regulation in neonates of shorebirds. Auk , 110, 445-457.
- Vleck, C.M. 1981. Hummingbird incubation: female attentiveness and egg temperature. Oecologia , 51, 199-205.
- Walsberg, G.E. 1983. Avian ecological energetics. In: Avian Biology (Ed. by D.S. Farner & J.R. King), pp. 161-220. New York: Academic Press.
- Walsberg, G.E. 1986. Thermal consequences of roost site selection: the relative importance of three modes of heat conservation. Auk , 103, 1-7.
- Webster, M.D. & Weathers, W.W. 1988. Effects of wind and air temperature on metabolic rate in Verdins, *Auriparus flaviceps*. Physiological Zoology , 61, 543-554.
- Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. Trends in Ecology and Evolution , 11, 384-388.
- Westerterp, K.R. & Bryant, D.M. 1984. Energetics of free existence in swallows and martins (Hirundinidae) during breeding: a comparative study using doubly labeled water. Oecologia , 62, 376-381.
- White, F.N. & Kinney, J.L. 1974. Avian incubation. Science , 186, 107-115.
- Whitfield, D.P. & Tomkovich, P.S. 1996. Mating system and timing of breeding in holarctic waders. Biological Journal of the Linnean Society , 57, 277-289.
- Wiebe, K.L. & Martin, K. 1997. Effects of predation, body condition and temperature on incubation rhythms of White-tailed Ptarmigan. Wildlife Biology , 3, 219-227.

- Wiersma,P. 1991. Living exposed and in the cold. Thermostatic costs of nearctic Knots (*Calidris canutus islandica*) as measured by means of heated taxidermic mounts. Masters thesis, University of Groningen
- Wiersma,P., Bruinzeel,L. & Piersma,T. 1993. Energy savings in waders: Studies on the insulation of Knots. Limosa , 66, 41-52.
- Wiersma,P. & Piersma,T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Wilkie,A.O.M. 1981. Incubation Rhythm and behaviour of a Dotterel *Charadrius morinellus* nesting in Norway. Ornis Fennica , 58, 11-20.
- Williams,J.B. 1996. Energetics of avian incubation. In: Avian energetics and nutritional ecology (Ed. by C.Carey), pp. 375-415. New York: Chapman & Hall.
- Williams,J.B. & Dwinell,B. 1990. Incubation energetics of female Savannah Sparrows. Physiological Zoology , 63, 353-372.
- Wolf,B.O. & Walsberg,G.E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. Ecology , 77, 2228-2236.
- Yom-Tov,Y. & Hilborn,R. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia , 48, 234-243.



## **Appendix A**

### **INCUBATION SCHEDULING IN THE EURASIAN DOTTEREL**

#### **Introduction**

There are several published descriptions of incubation schedules, especially for shorebirds, including data for Eurasian dotterel, that describe how incubation scheduling parameters vary with the parental care system, time of day, darkness or daylight, weather conditions, stage of breeding and between individuals (Parmelee 1970; Norton 1972; Wilkie 1981; Cartar & Montgomerie 1985; Løfaldli 1985; Kálás 1986; Cartar & Montgomerie 1987; Miskelly 1989; Pulliainen & Saari 1994; Pulliainen & Saari 1997). This study recorded 10,574 trips off the nest over 723 days of recorded incubation scheduling from 46 nests and these relatively large sample sizes allow better quantification of the pattern of incubation scheduling. In this appendix I explicitly test some of the hypotheses that are often implicit in other descriptive studies of incubation scheduling in shorebirds. In Chapters 3 and 4, hypotheses were tested of how incubation varies with ecological factors. This appendix also gives the descriptive data on incubation scheduling that underlies the results described in these chapters.

Firstly, I investigate how incubation scheduling varies between parental care systems. By sharing duties, the males at biparental nests will have smaller energetic costs of incubation and greater off-duty time in which to forage, so that parents that share incubation should be less energetically constrained than uniparental males. This allows investigation of how incubation scheduling varies under different degrees of energetic constraint. Also, the function of some periods of inattendance may differ between parental care systems as some absences may represent parent changeovers and this could produce different patterns of incubation scheduling.

Next I examine how incubation scheduling varies with the time of day and whether it is light or dark. If the activity of nest predators varies with the light conditions and the parent's presence at the nest can affect the probability of clutch predation either by changing the difficulty with which the nest can be found (Cartar & Montgomerie 1985) or through nest defence (Baerends

et al. 1970; e.g. Harvey 1971; Inglis 1977), or because the parent's movements to and from the nest help the predator to find the nest (Erikstad et al. 1982; Wiebe & Martin 1997; Martin & Ghalambor 1999), then the pattern of nest attendance might be expected to vary with time of day or the light level (Cartar & Montgomerie 1985). Weather conditions and, consequently the rate at which unattended eggs cool, vary with time of day (Chapter 3). Concentrating feeding trips during the times of day when unattended eggs would cool most slowly could decrease both the energetic cost of rewarming the eggs and the amount of time that the embryos spend cooled below a temperature suitable for development. As well as investigating how incubation scheduling varied with the time of day and so the typical daily pattern of variation in egg cooling rates, I also investigated how incubation scheduling varied directly with egg cooling rate.

Incubation scheduling may vary with stage of incubation if the thermal tolerance of embryos varies (Batt & Cornwell 1972) or if parents body reserves are depleted so that they cannot buffer periods of energetic shortfall (Chapter 3; Holt et al. 2002): here I investigate how incubation scheduling varies through the incubation period.

There may be differences in the incubation scheduling between uniparental nests if the parents experience different degrees of energetic constraint. Different nest microclimates may give parents different energetic costs of incubation and thermoregulation and, as the level of body reserves varied between incubating males, they may be able to supplement their energy budgets using body reserves to different degrees (Chapter 3). Also, incubation scheduling may vary if individuals differ in their foraging ability, allowing some individuals to spend less time foraging and more time on the nest (Cartar & Montgomerie 1985). I investigate whether nest attendance varied with the nest microclimate in terms of exposure to wind, which would affect both the parent's cost of thermoregulation (Wiersma & Piersma 1994) and the rate of cooling of unattended eggs (Chapter 3). I also test whether nest attendance varies with the size of the nest, as larger nests could contain more insulating nest lining (Chapter 6) and possibly more of the parents body, which may reduce thermoregulatory costs (Calder 1973).

There are various measures of incubation scheduling. In this appendix I present data on trip duration, incubation bout duration, trip frequency and nest attendance. Clearly these variables are interdependent but I present data on all four to investigate the exact manner in which dotterel adjust their incubation scheduling. In addition, I examine the proportion of time that eggs spent below a temperature suitable for embryonic development (using 20°C as an index of their unknown physiological zero temperature, Chapter 4) and the energetic costs of incubation, probably the two most important consequences of variation in incubation scheduling.

Avian embryos are probably more susceptible to damage from exposure to high temperatures (when the eggs are hotter than 42°C) than to exposure to low temperatures (Webb 1987). Birds, including shorebirds and other Charadriiformes, that nest in warm microclimates show a variety of mechanisms to prevent their embryos overheating such as standing over the nest, egg-wetting (although, these last two may principally serve to prevent the parent rather than the embryos from overheating) and covering the eggs while unattended with sand or other materials (Drent 1970; Purdue 1976 & references therein; Grant 1982; Cramp & Simmons 1983; Downs & Ward 1997). In addition, incubation may be scheduled to ensure that the nest is not unattended during intense solar radiation, which is the most likely source of embryonic overheating in most habitats (Purdue 1976; Zerba & Morton 1983). In Chapter 3, I tested hypotheses of how incubation scheduling might vary with a number of constraints but did not formulate any hypothesis of how incubation scheduling might vary with the risk of embryonic overheating. In this appendix I investigate whether dotterel's embryos were ever at risk of overheating.

## **Methods**

Data on incubation scheduling were collected in 1997 and 1998 from two low-alpine (Horsfield & Thompson 1996) sites, separated by 8km, in the Central Highlands of Scotland. Nest attendance and weather data were collected as described in Chapter 3. The power for incubation, steady state incubation and thermoregulation, egg temperature and egg cooling

rate and the consequent power for incubation were estimated as described in Chapter 3. The observer was licensed to disturb nesting dotterel. The date that a clutch was initiated (first egg date) was observed, estimated from hatch date (assuming a 28 day period from first egg laid to last chick hatched, Cramp & Simmons 1983; D.P. Whitfield unpublished data) or estimated from an equation relating egg density to days until hatch (derived from measurements of clutches of known hatch date, D.P. Whitfield unpublished data).

Statistical tests were carried out using SPSS (Norusis 1990). Two-tailed probabilities are given. Means are quoted  $\pm$  95% confidence limits or, for non-normally distributed variables, medians  $\pm$  95% confidence limits calculated using Nair's table (Campbell 1989).

**Summary of results**

As a large number of analyses are presented in this appendix, their results are summarised in Table 1 and then detailed in the following text.

Table 1. Summary of the results of analyses in Appendix A.

	dependent variable>	nest attendance	trip duration	incubation		proportion		power for incubation
				bout duration	trip frequency	of time below 20°C	incidence of egg neglect	
parental care system		biparental> uniparental	uniparental> biparental	biparental> uniparental	uniparental> biparental	uniparental> biparental	uniparental> biparental	=
time of day	uniparental	yes	yes	yes	yes	yes	yes	yes
	biparental	yes	=	yes	yes	yes	=	yes
daylight & darkness	uniparental	dark>light	light>dark	dark>light	=	=	light>dark	dark>light
	biparental	light>dark	=	=	=	dark>light	=	dark>light
rate of egg cooling	uniparental	=	=	+	-	+	+	=
	biparental	+	=	=	-	+	=	+
stage of incubation	uniparental	-	=	-	+	+	-	=
	biparental	+	=	=	-	-	(=)	-

	wind exposure		
	body reserves	nest size	of nest site
sources of variation in attendance between nests	+	+	=

Do uniparental dotterel use trip duration or trip frequency to vary nest attendance?

with time of day trip frequency and trip duration

between nests trip duration

Dotterel embryos were never at risk from overheating while unattended

= indicates no significant variation or difference with independent variable

+ indicates a significant & positive correlation

- indicates a significant & negative correlation

yes indicates significant variation with a categorical variable

where two samples are compared we indicate the direction of any significant difference

## Parental care

### *Nest attendance*

Biparental nests were attended significantly more than uniparental nests, whether comparing on a matched pair basis (Chapter 4) or as independent samples (t-test:  $t_{41}=5.595$ ,  $P<0.001$ , uniparental  $0.82 \pm 0.02$ , biparental  $0.94 \pm 0.01$ , Fig. 1). Uniparental nests were attended  $81.5\% \pm 2.0\%$  of the time and biparental nests for  $93.9\% \pm 1.4\%$  (based on means of daily means for 38 uniparental and eight biparental nests).

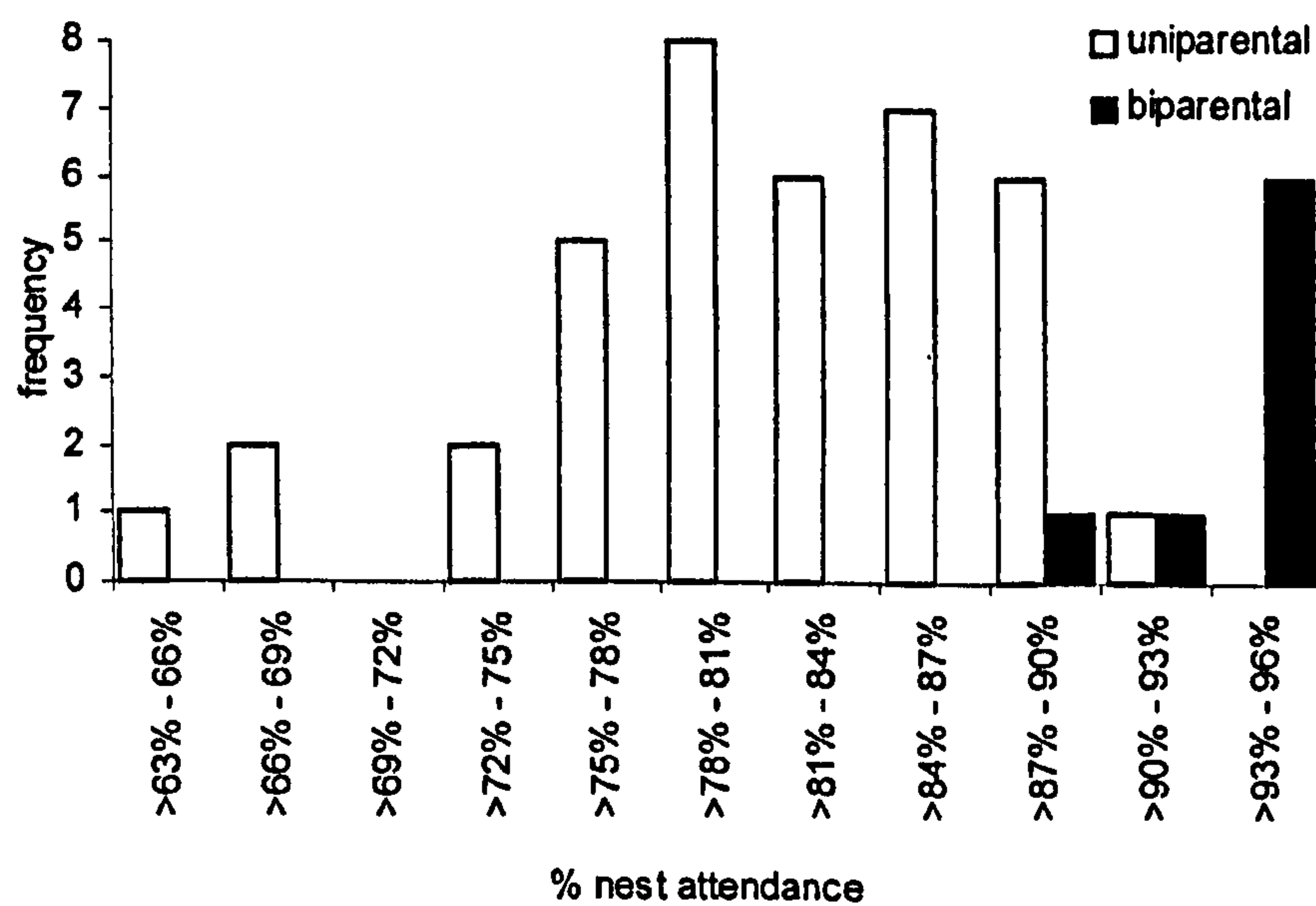
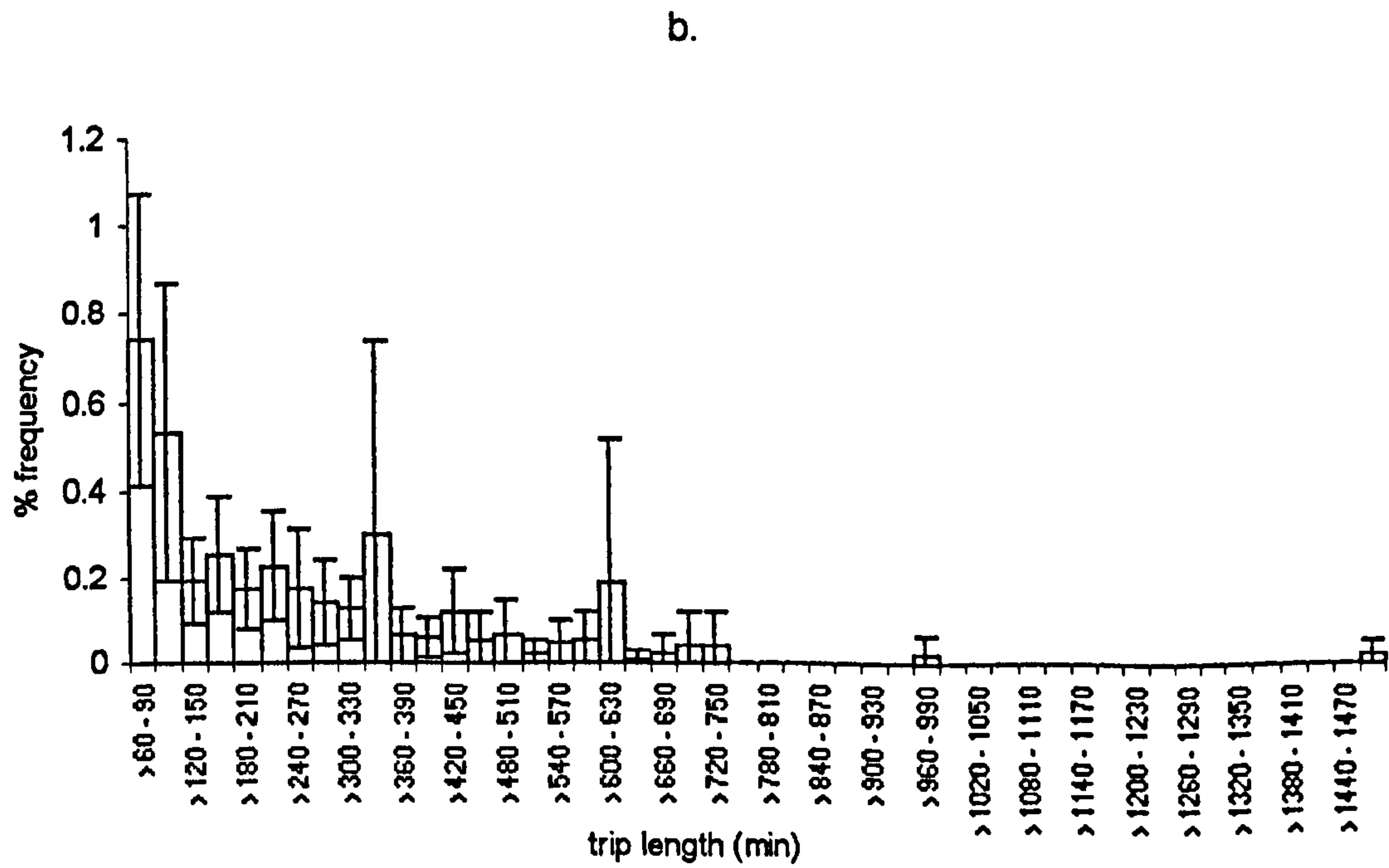
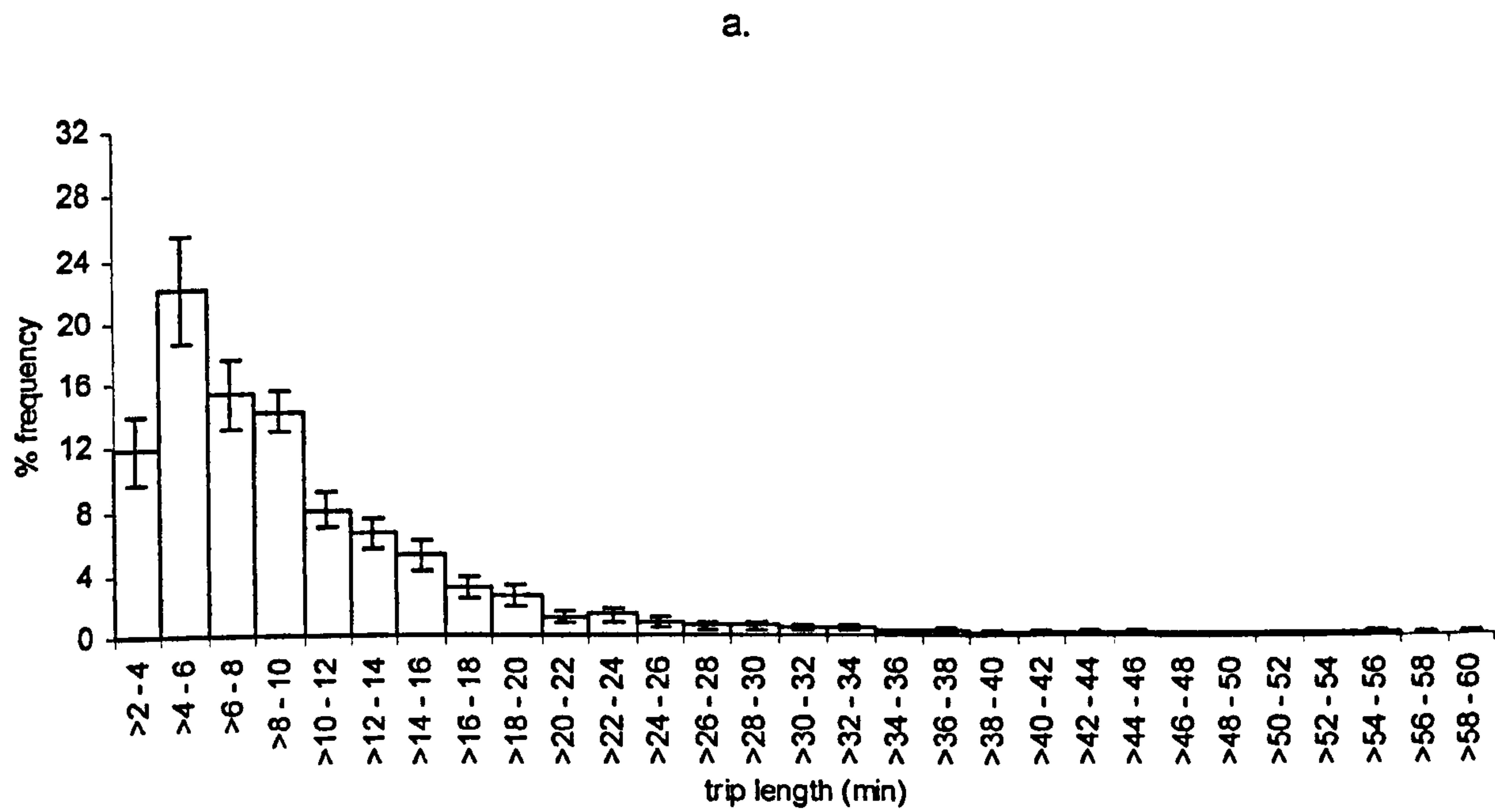


Figure 1. Percentage nest attendance with parental care system (nest mean of daily mean for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

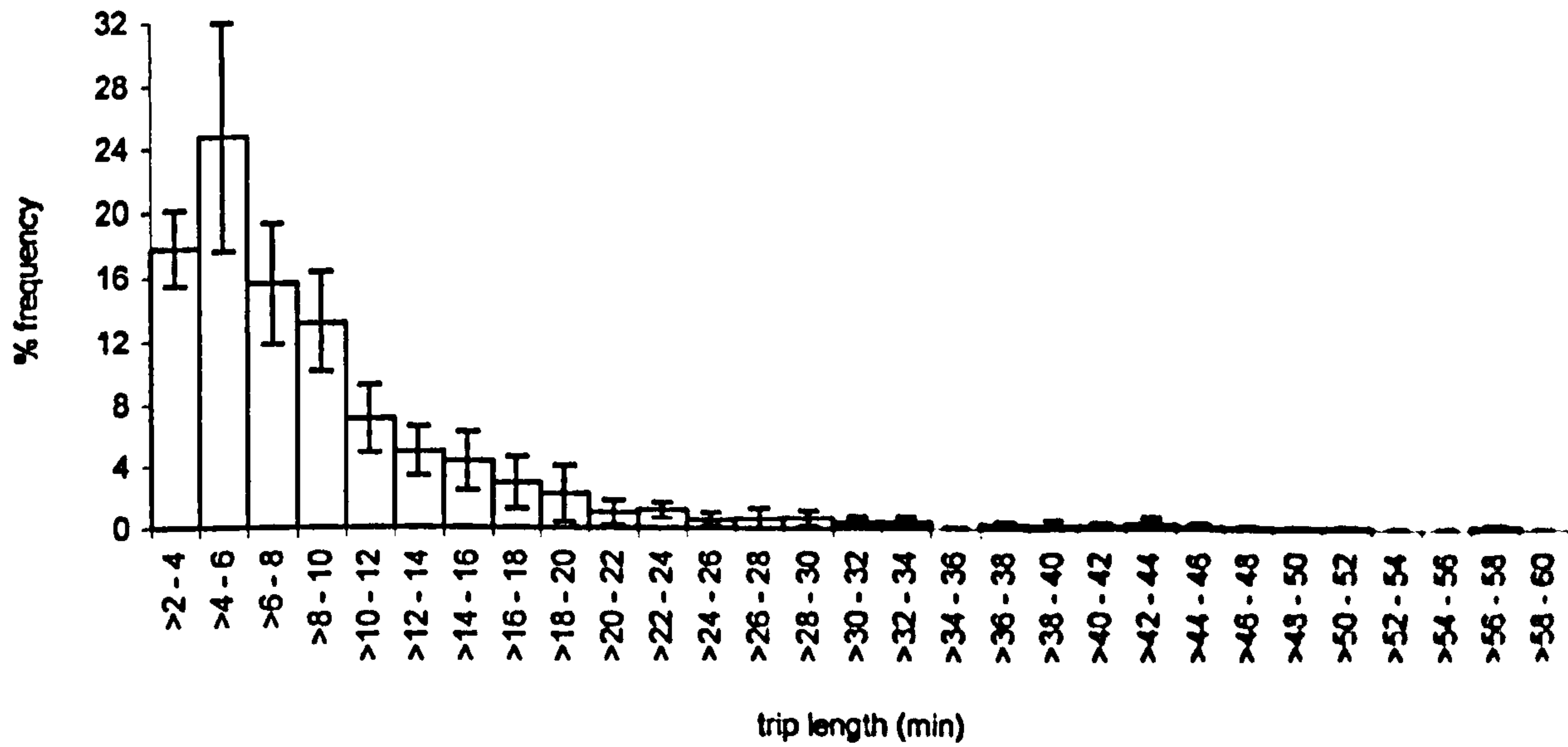
*Trip duration*

The distribution of trip lengths was highly skewed (Figs. 2a, 2b, 3a & 3b).

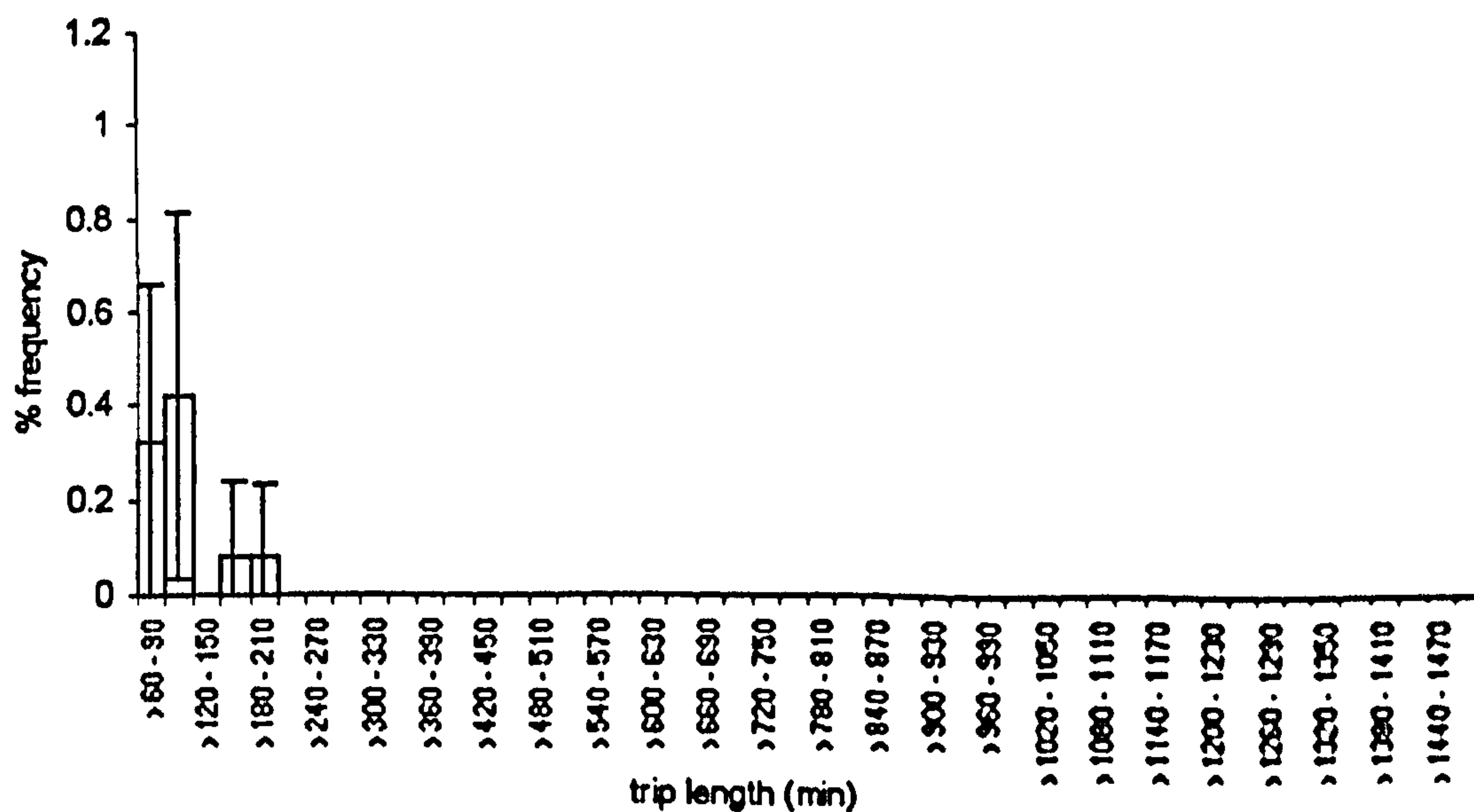


Figures 2a and 2b. Trip lengths of uniparental nests (mean  $\pm$  95% percentage frequency, the frequency distribution was drawn as two graphs to allow the rare longer trips to be shown, based on a mean of  $240 \pm 47$  trips per nest from 38 nests).

a.



b.



Figures 3a and 3b. Trip lengths of biparental nests (mean  $\pm$  95% percentage frequency for eight nests, the frequency distribution was drawn as two graphs to allow the rare longer trips to be seen, based on a mean of  $183 \pm 60$  trips per nest from eight nests).

Although median trip length was clearly not normally distributed (Figs. 2a, 2b, 3a & 3c), the median of daily medians calculated for each nest approximated a normal distribution (Kolmogorov-Smirnov test comparing to the normal distribution: uniparental  $Z=0.744$ ,  $N=38$ ,



$P=0.744$ ; too little data for a valid test on the eight biparental nests, Fig. 4). Trips were significantly longer from uniparental nests than biparental nests (Chapter 3).

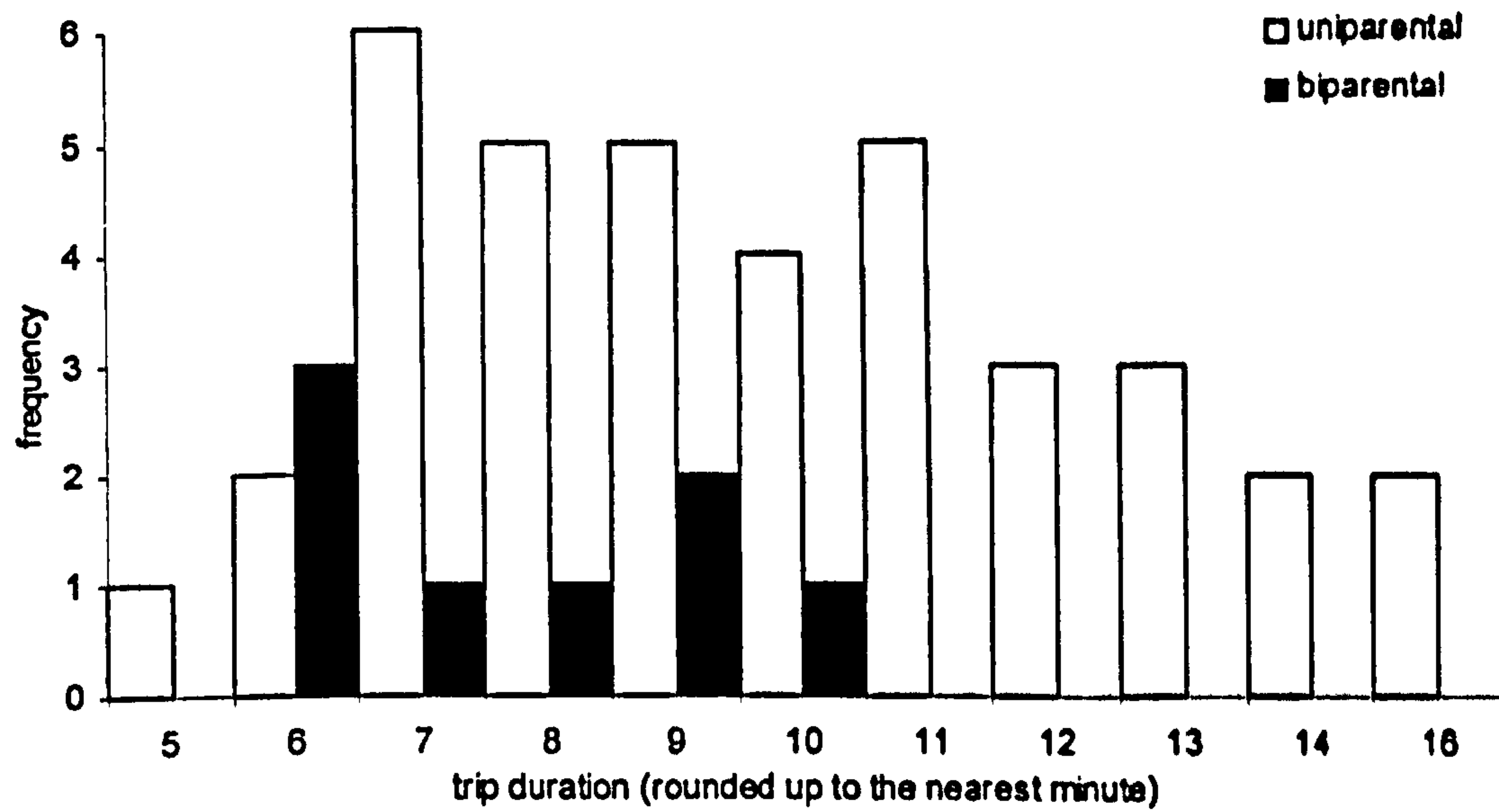


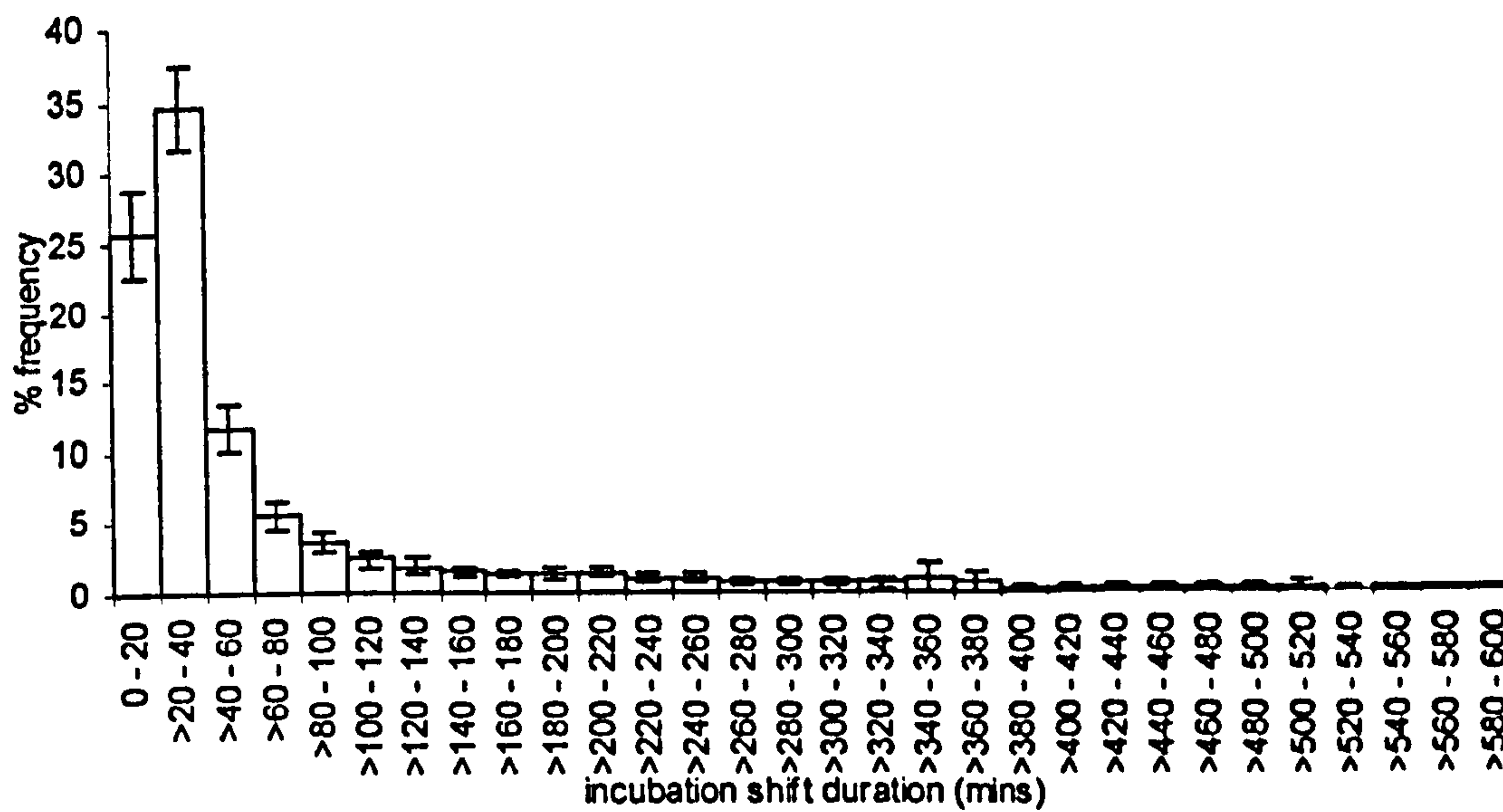
Figure 4. Trip duration and parental care (nest median of daily medians for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

Although, for consistency, the term 'trip' is used to describe periods of inattendance at biparental as well as uniparental nests, if some trips represent changeovers of parents sharing duties, they might better be described for biparental nests as nest absences.

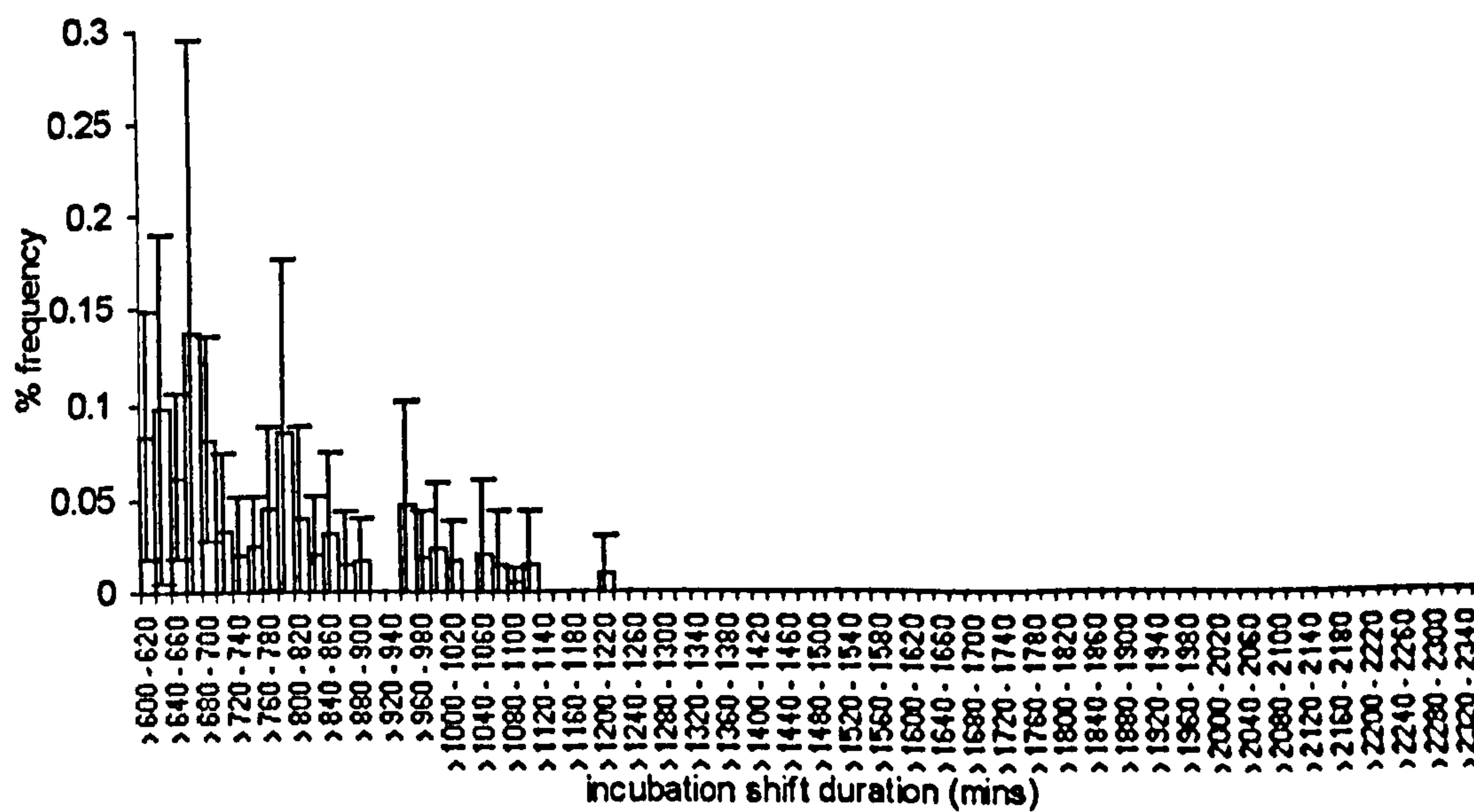
*Incubation bout duration*

The distribution of incubation bout durations was highly skewed (Figs. 5a, 5b, 6a & 6b.).

a.

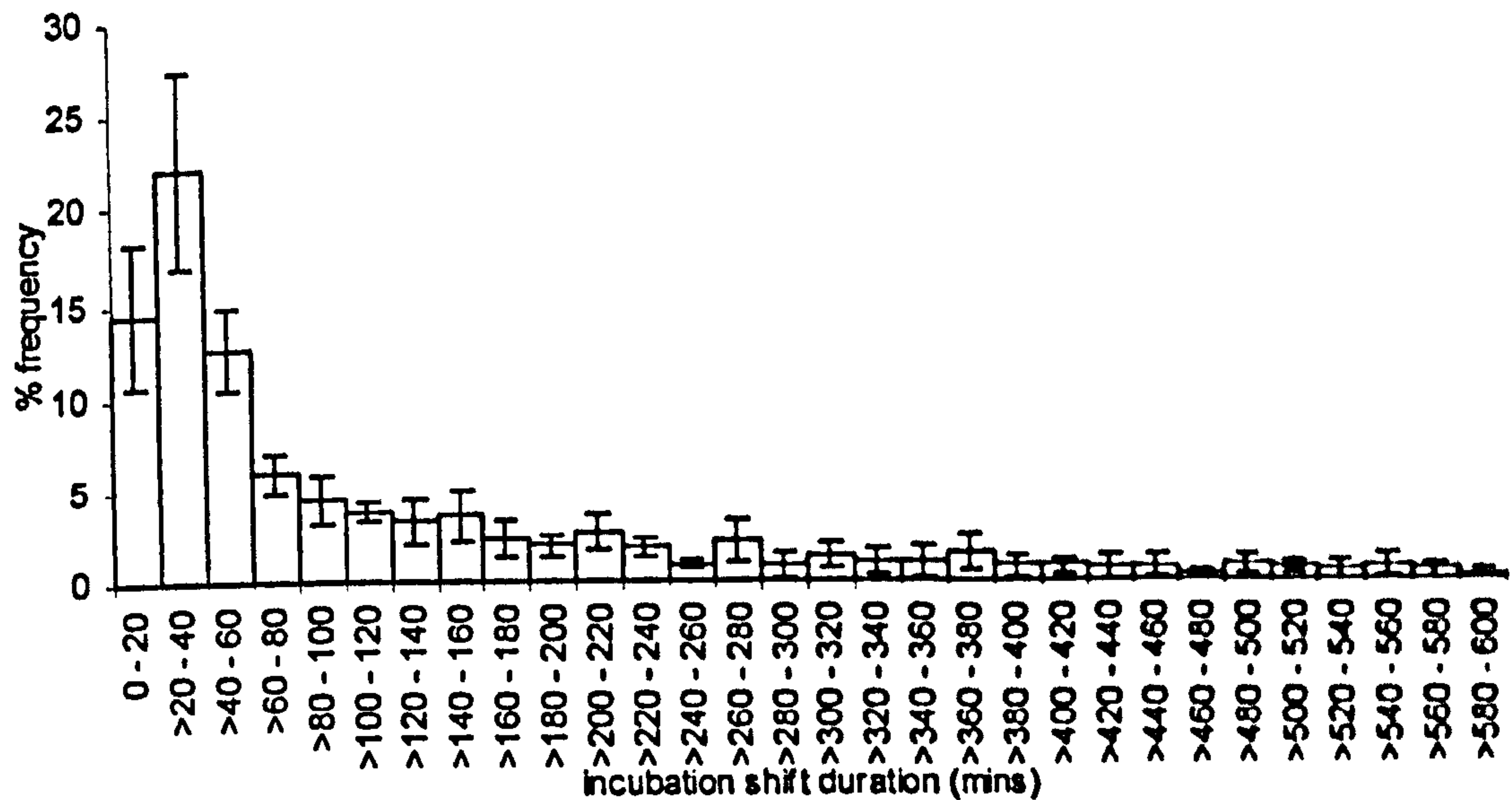


b.

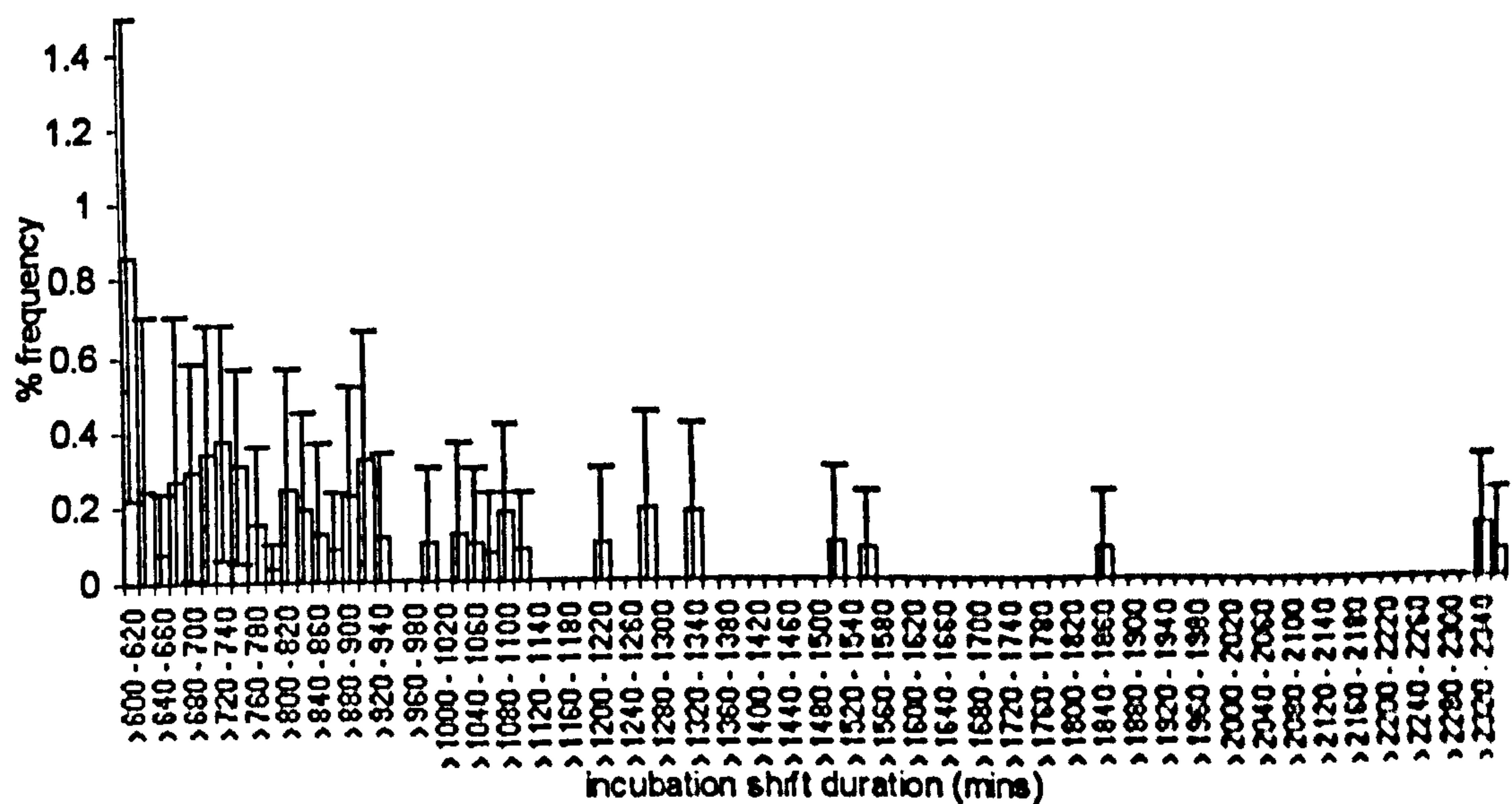


Figures 5a and 5b. Incubation bout durations of uniparental nests (mean  $\pm$  95% percentage frequency for 38 nests, the frequency distribution was drawn as two graphs to allow the rare longer trips to be shown).

a.



b.



Figures 6a and 6b. Incubation bout durations of biparental nests (mean  $\pm$  95% percentage frequency for 8 nests, the frequency distribution was drawn as two graphs to allow the rare longer trips to be seen).

Incubation bouts were significantly longer at biparental nests than uniparental nests (T-test:  $t'_{7.365}=3.446$ ,  $P=0.010$ , uniparental nests  $40.5 \pm 4.5$  min, biparental  $89.9 \pm 27.7$  min, the nest medians of daily medians used in this test approximated a normal distribution; Komogorov-Smirnov test comparing the sample distribution with a normal distribution: uniparental  $K=1.099$ ,  $N=38$ ,  $P=0.178$ , too few biparental nests for valid test, Fig. 7).

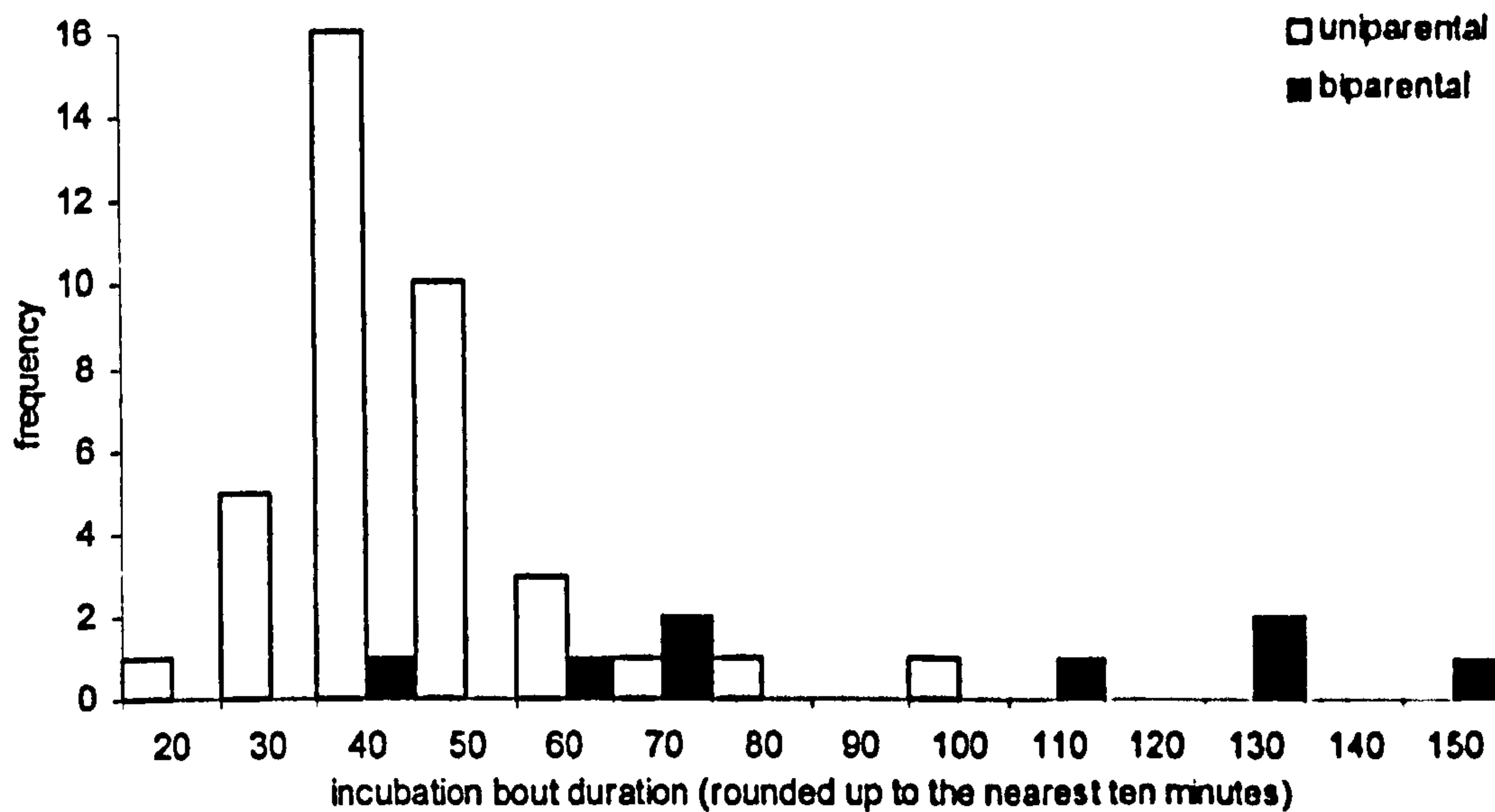


Figure 7. Incubation bout duration and parental care system (nest median of daily medians for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

#### Trip frequency

The frequency of trips from uniparental nests was significantly higher than from biparental nests (T-test:  $t_{44}=3.637$ ,  $P=0.001$ , mean trip rate from uniparental nests  $0.68 \pm 0.07\text{hr}^{-1}$ , biparental nests  $0.39 \pm 0.11 \text{hr}^{-1}$ , Fig. 8).

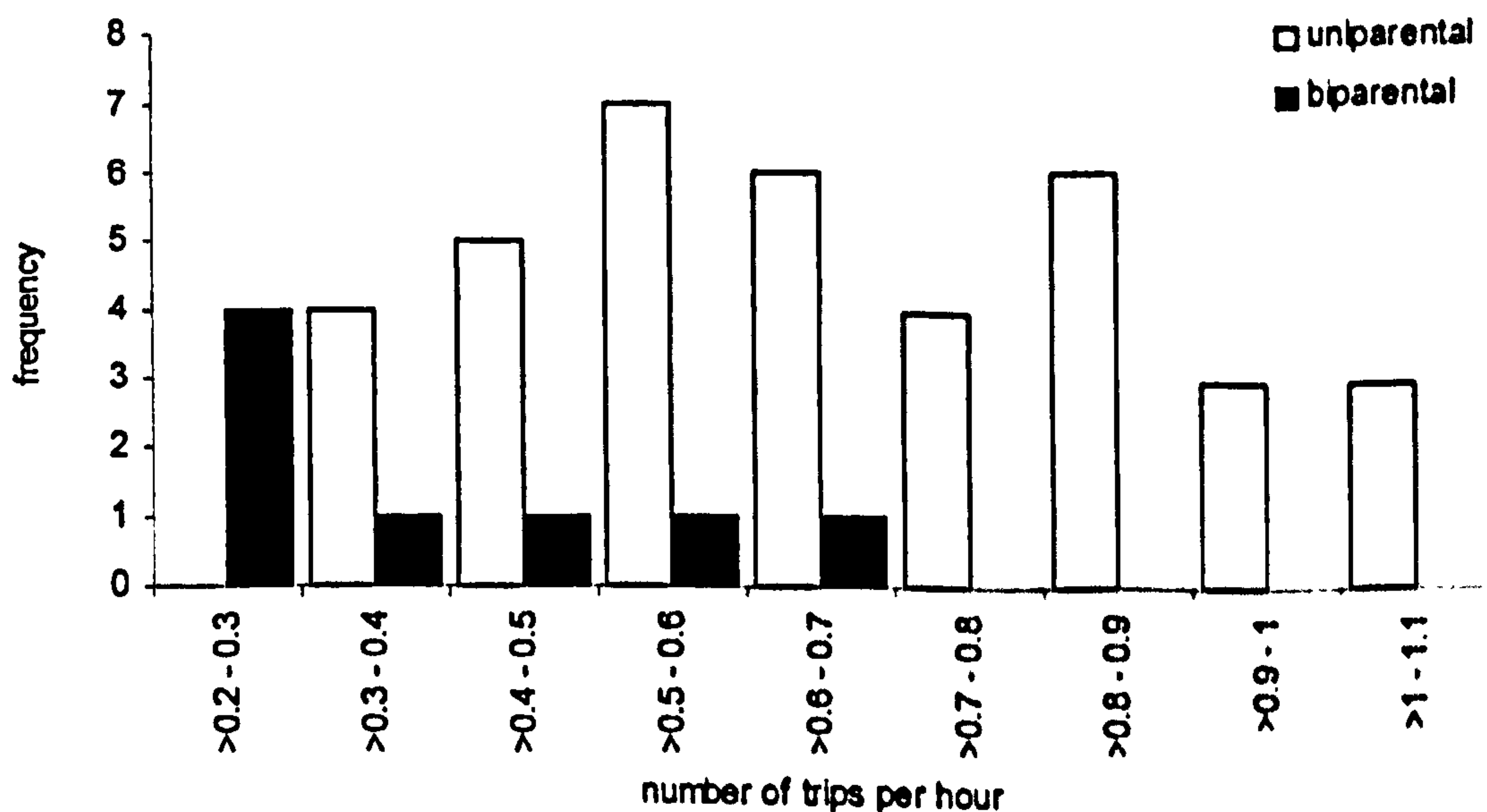


Figure 8. Trip frequency and parental care system (nest mean of daily mean for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

### *Proportion of time eggs below 20°C*

The eggs of biparental nests spent significantly less time below 20°C than those of uniparental nests (Chapter 3, Fig. 9): uniparental nests  $10.8\% \pm 2.6\%$  of time below 20°C and biparental nests  $2.0\% \pm 0.8\%$  (based on the mean of daily means for 38 uniparental and eight biparental nests).

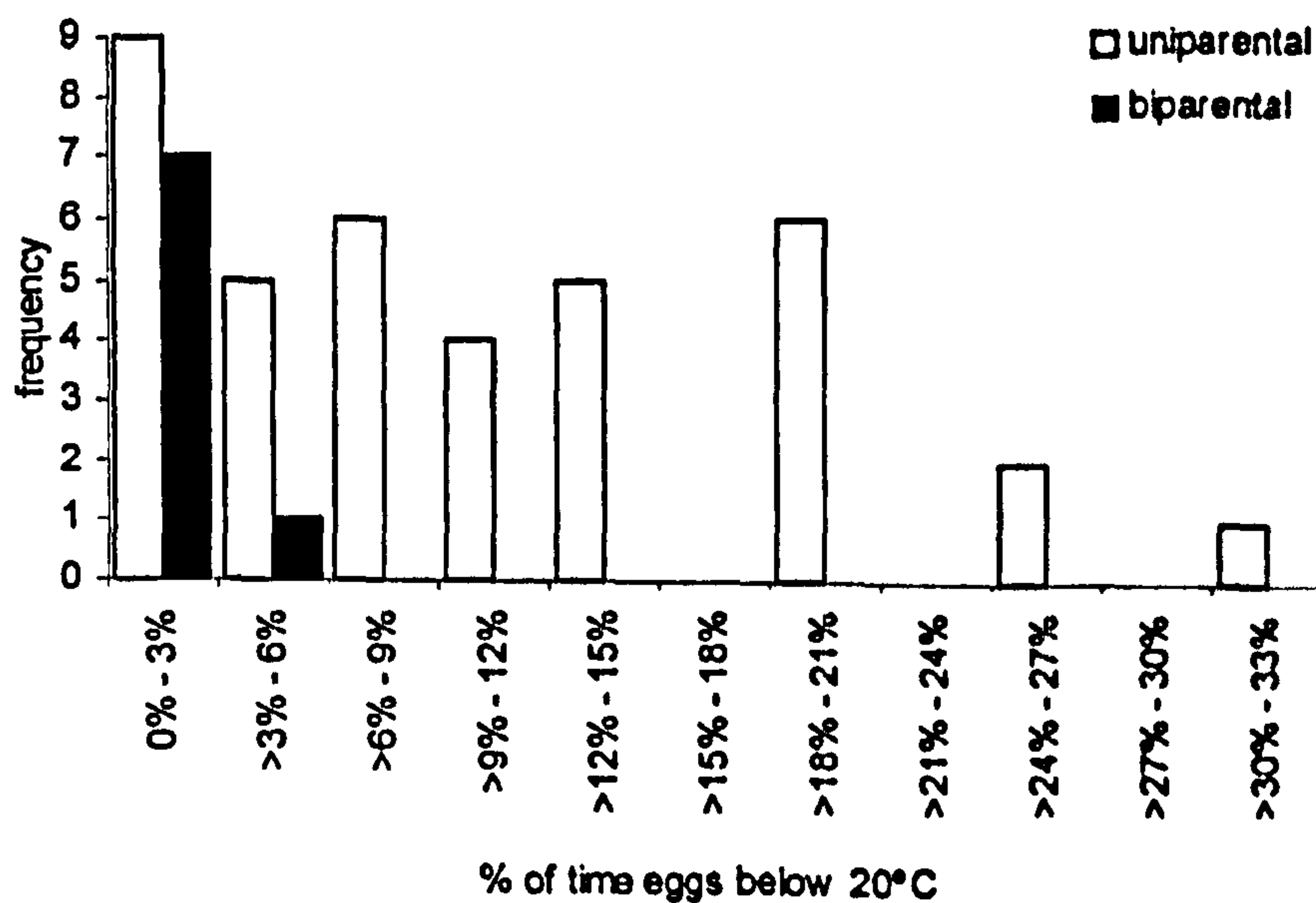


Figure 9. Estimated percentage of time that eggs spent below 20°C with parental care system (nest mean of daily mean for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

### *Incidence of egg neglect*

Uniparental nests were neglected (defined as not attended for more than 2h) more frequently than biparental nests (Chapter 4, Fig. 10). Biparental nests were neglected  $0.011 \pm 0.014$  times per day or on  $1.0\% \pm 1.3\%$  of days and uniparental nests  $0.295 \pm 0.092$  times per day or on  $23.3 \pm 6.9\%$  of days (based on the entire sample of 38 uniparental nests and eight biparental nests: confining the sample to only nests with at least five days recorded, uniparental nests were neglected on  $23.2\% \pm 7.2\%$  of days, biparental nest sample unchanged). Nests were infrequently neglected more than once per day (uniparental nests were neglected twice on  $7.0\% \pm 4.7\%$  days when they were neglected,  $N=27$  nests where

neglect was recorded; biparental nests were never neglected more than once in a day,  $N=2$  nests where neglect was recorded).

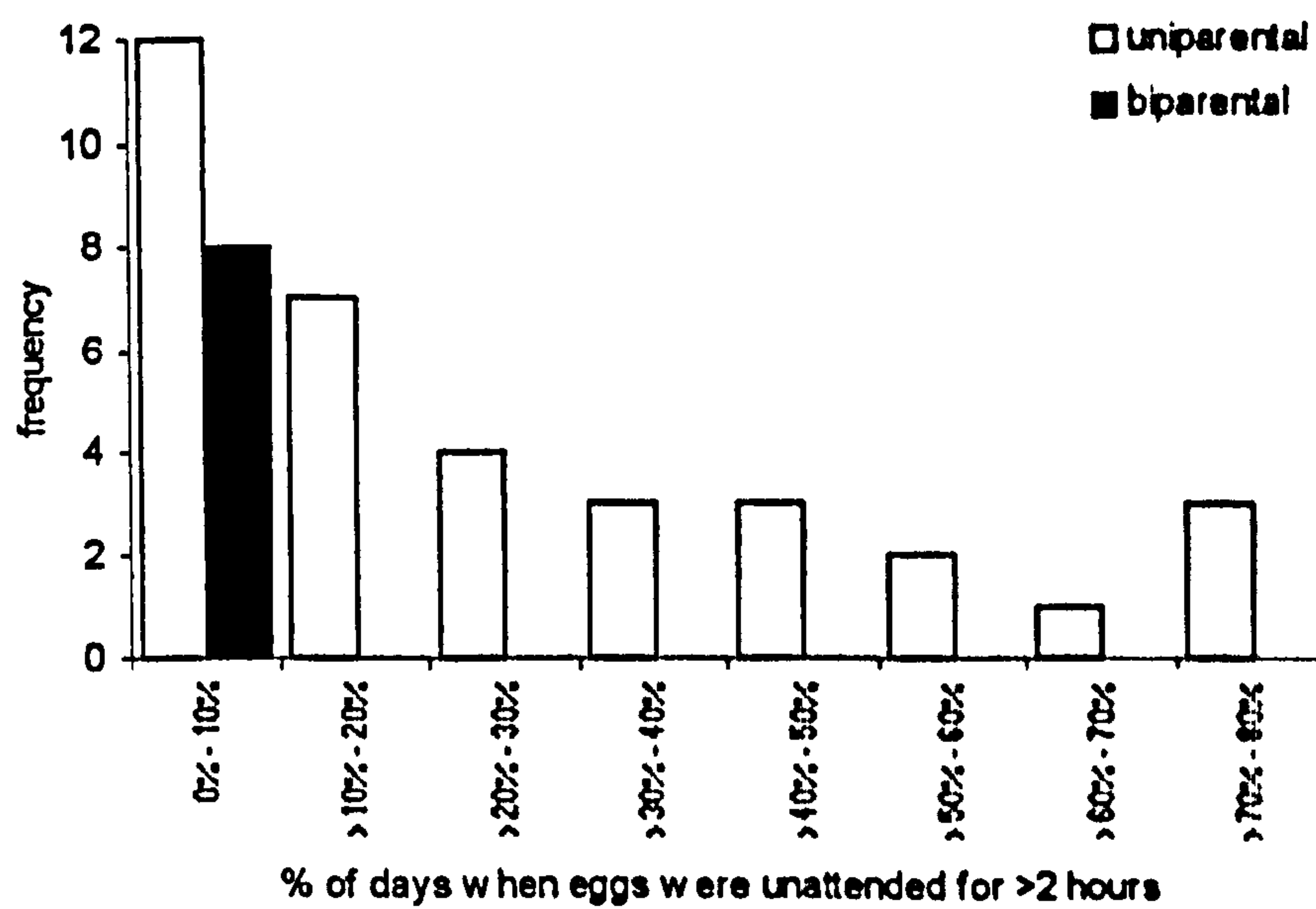


Figure 10. The percentage of days on which eggs were neglected and the parental care system (for 35 uniparental and eight biparental nests with at least five days at least 75% logged).

#### *Power for incubation*

There was no significant difference in the estimated energy expended to incubate uniparental and biparental nests (Chapter 3, Fig. 11). At uniparental nests  $0.97 \pm 0.03W$  was expended and at biparental nests  $0.92 \pm 0.05W$  was expended (based on the means of daily means for 38 uniparental and eight biparental nests).

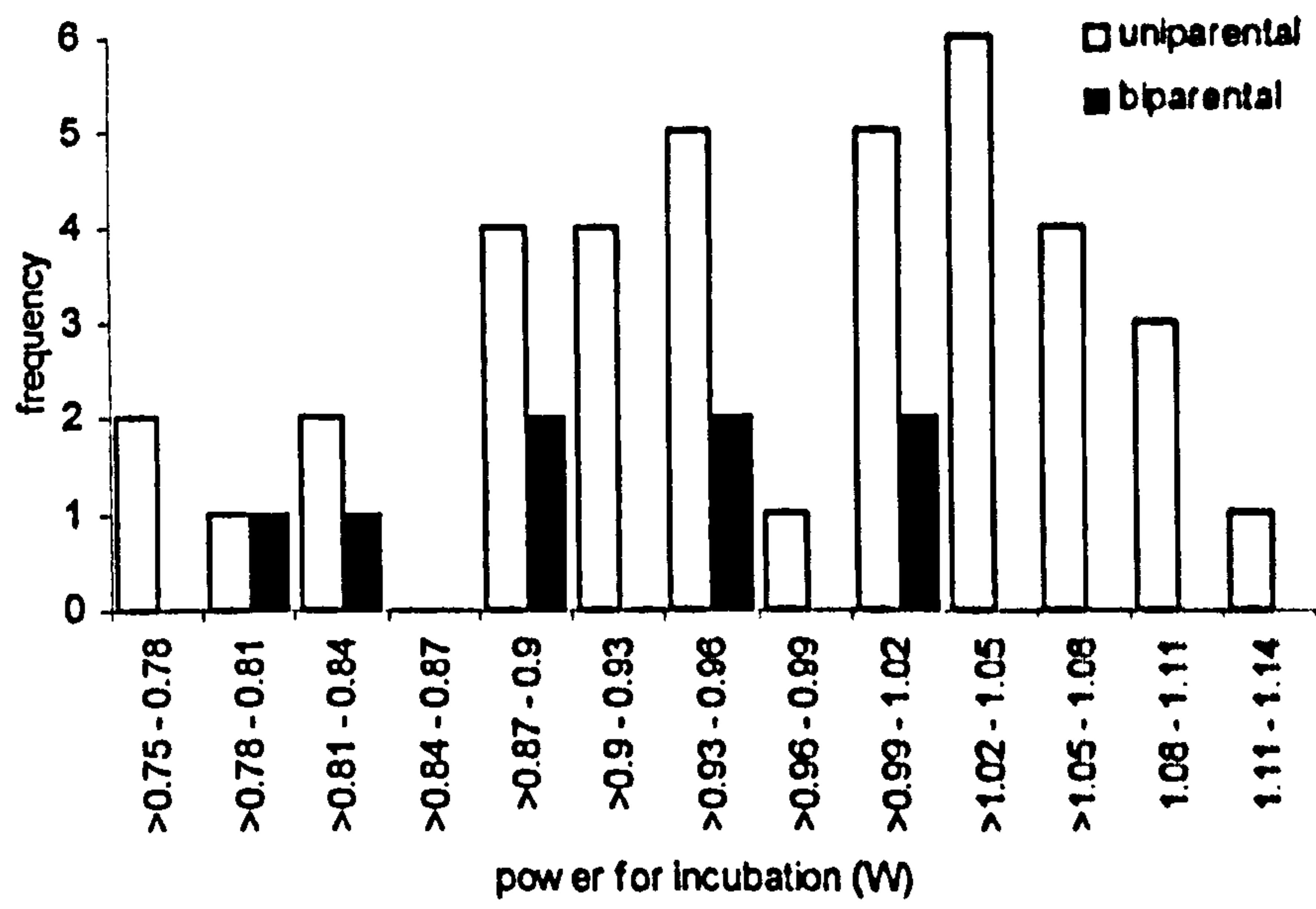


Figure 11. Estimated power for incubation and parental care system (nest mean of daily mean for days at least 75% logged, for 38 uniparental nests and eight biparental nests).

## Time of day

### *Nest attendance*

Figure 9 in Chapter 3 shows the pattern of nest attendance in relation to time of day for both uniparental and biparental nests. Attendance of uniparental nests varied significantly with hour of day over the whole day (GLM of attendance: hour  $F_{23,851}=32.093$ ,  $P<0.001$ , partial  $R^2=0.464$ ; nest identity  $F_{37,851}=6.991$ ,  $P<0.001$ , partial  $R^2=0.233$ , model  $R^2_{adj}=0.507$ ), during daylight (GLM of attendance: hour  $F_{18,664}=38.797$ ,  $P<0.001$ , partial  $R^2=0.513$ ; nest identity  $F_{37,664}=7.199$ ,  $P<0.001$ , partial  $R^2=0.286$ , model  $R^2_{adj}=0.558$ ), and during darkness (GLM of attendance: hour  $F_{8,166}=44.144$ ,  $P<0.001$ , partial  $R^2=0.615$ ; nest identity  $F_{37,166}=5.721$ ,  $P<0.001$ , partial  $R^2=0.560$  model  $R^2_{adj}=0.685$ ).

Attendance of biparental nests also varied significantly with hour of day over the whole day (GLM of attendance: hour  $F_{23,161}=5.372$ ,  $P<0.001$ , partial  $R^2=0.434$ ; nest identity  $F_{7,161}=7.260$ ,  $P<0.001$ , partial  $R^2=0.240$  model  $R^2_{adj}=0.430$ ), during daylight (GLM of attendance: hour  $F_{18,125}=2.450$ ,  $P=0.002$ , partial  $R^2=0.261$ ; nest identity  $F_{7,125}=8.909$ ,  $P<0.001$ , partial  $R^2=0.333$  model  $R^2_{adj}=0.558$ ), and during darkness (GLM of attendance: hour  $F_{8,31}=8.241$ ,  $P<0.001$ , partial  $R^2=0.615$ ; nest identity  $F_{7,31}=4.525$ ,  $P=0.001$ , partial  $R^2=0.505$  model  $R^2_{adj}=0.661$ ).

Dotterel may vary trip duration, incubation bout duration and/or trip frequency to alter their nest attendance. Trip duration, incubation bout duration and trip frequency will not vary independently of each other, however, and including any two in an analysis will describe all variation in the third. Hourly uniparental nest attendance varied significantly with both trip frequency and trip duration (GLM of % attendance: trip frequency  $F_{1,21}=44.329$ ,  $P<0.001$ , partial  $R^2=0.679$   $\beta=-0.225$ ; trip duration  $F_{1,21}=9.826$ ,  $P=0.005$ , partial  $R^2=0.319$   $\beta=-0.0251$ , model  $R^2_{adj}=0.859$ , using the mean of nest means of hourly attendance and trip frequency and the median of nest medians of trip duration)



### *Trip duration*

Median trip length varied significantly with time of day in uniparental nests but not in biparental nests, although a smaller sample size gave less statistical power for the latter test (Kruskal Wallis testing whether median trip length varied with the hour of the day, uniparental:  $\chi^2_{23}=70.984$ ,  $P<0.001$ , where available, we included a summary datum per nest in each hour category, between 29 and 37 of the 38 nests each contributing a median trip length datum per hour of the day, biparental:  $\chi^2_{23}=26.379$ ,  $P=0.283$ , seven or eight of the eight nests each contributing a median trip length datum per hour of the day). This test was imperfectly balanced but because each hour category had data from means of 93% and 99% of nests for uniparental and biparental nests, respectively, it is unlikely that the test was biased by the disproportionate influence of any nests. Trips appeared to be longer during the middle of the day at uniparental nests (Fig. 12). No trend was apparent for biparental nests, possibly because estimates were poorer due to smaller sample sizes (Fig. 13).

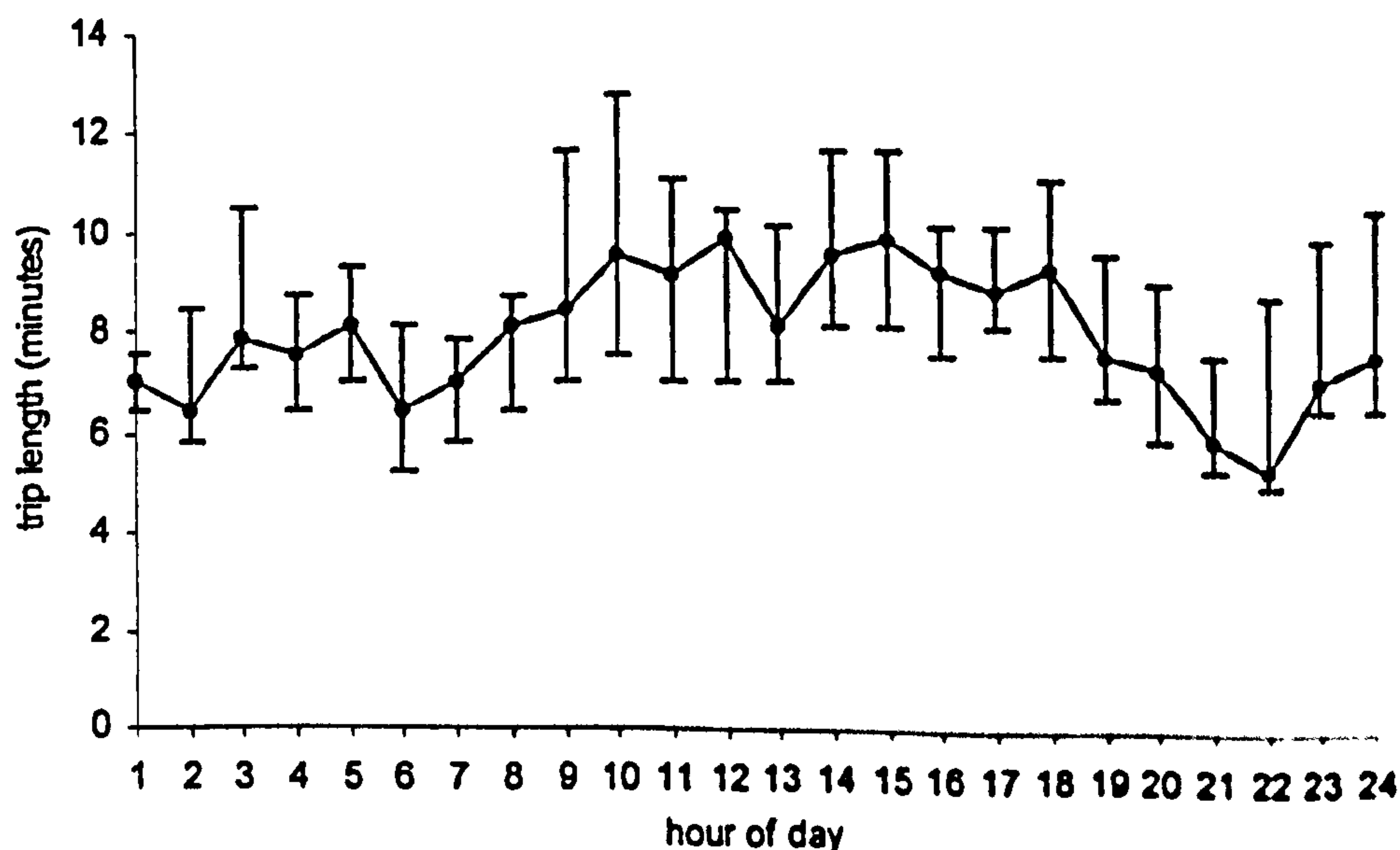


Figure 12. Trip duration for uniparental nests with time of day (medians  $\pm$  95% c.i. were calculated from the median values from between 29 and 37 nests for each hour of the day).

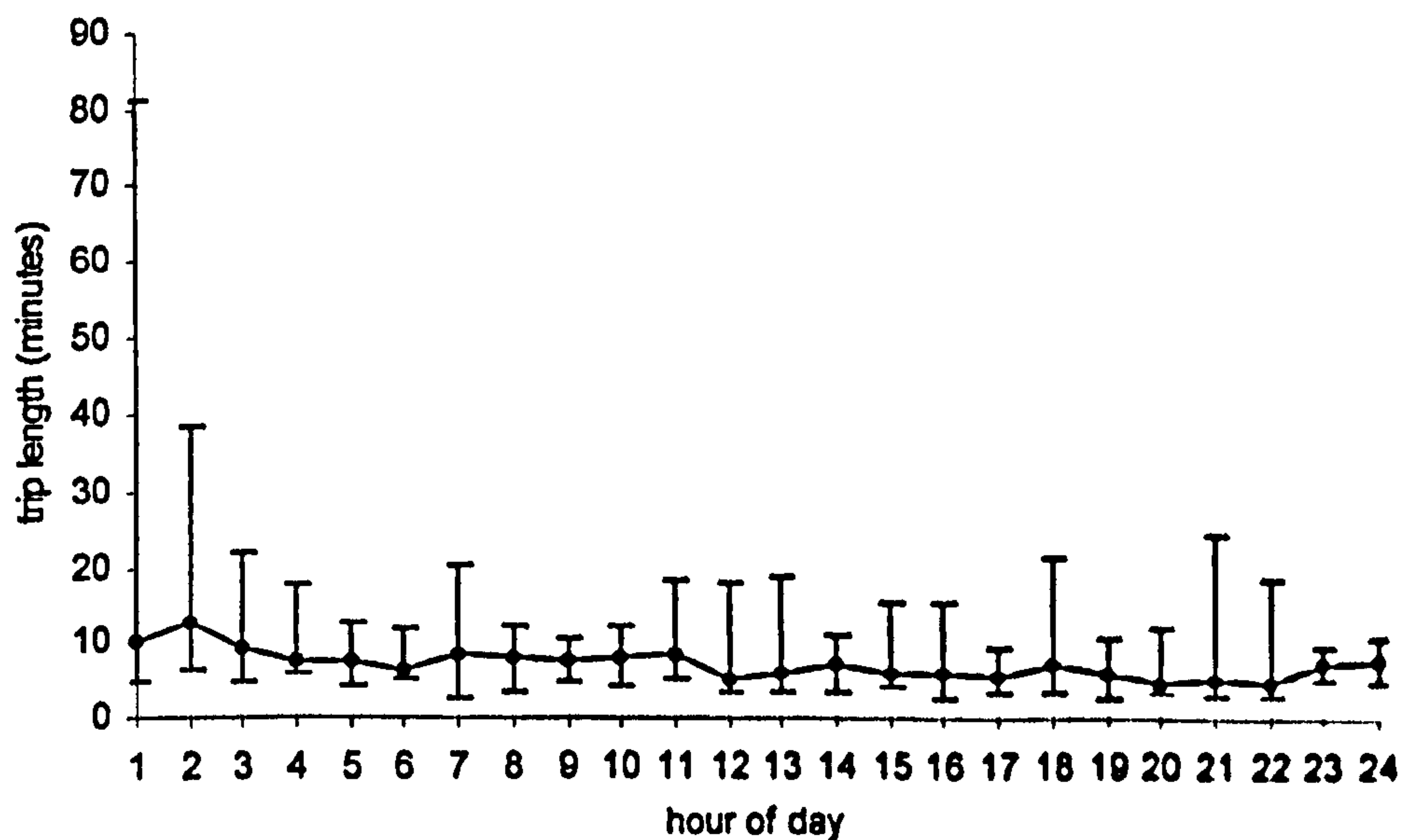


Figure 13. Trip duration for biparental nests with time of day (medians  $\pm$  95% c.i. were calculated from the median values from either seven or eight nests for each hour of the day).

#### *Incubation bout duration*

Median incubation bout duration varied significantly with time of day in both uniparental nests and biparental nests (Kruskal Wallis testing whether median incubation bout duration varied with the hour of the day, uniparental:  $\chi^2_{23}=364.211$ ,  $P<0.001$ , where available, we included a summary datum per nest in each hour category, between 29 and 37 of the 38 nests each contributing a median trip length datum per hour of the day, biparental:  $\chi^2_{23}=40.904$ ,  $P=0.012$ , seven or eight of the eight nests each contributing a median trip length datum per hour of the day). This test was imperfectly balanced but because each hour category had data from means of 92% and 98% of nests for uniparental and biparental nests, respectively, it is unlikely that the test was biased by the disproportionate influence of any nests. The shortest incubation bouts appeared to be initiated during the middle of the day, before dawn and after dusk at uniparental nests but the pattern was less clear for biparental nests (Figs. 14 & 15).

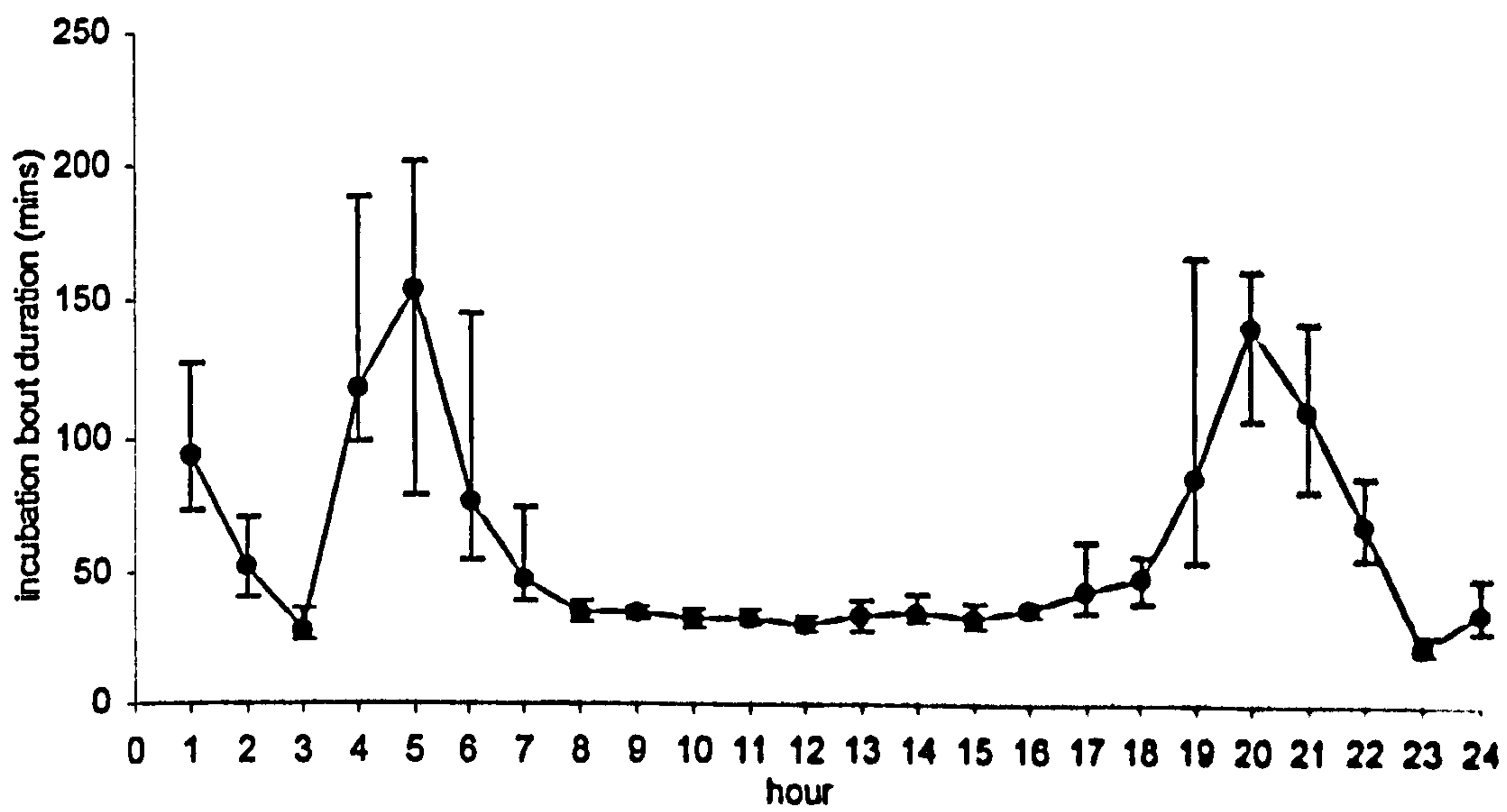


Figure 14. Incubation bout duration for uniparental nests with time of day (medians  $\pm$  95% c.i. were calculated from the median daily values from between 28 and 38 nests for each hour of the day).

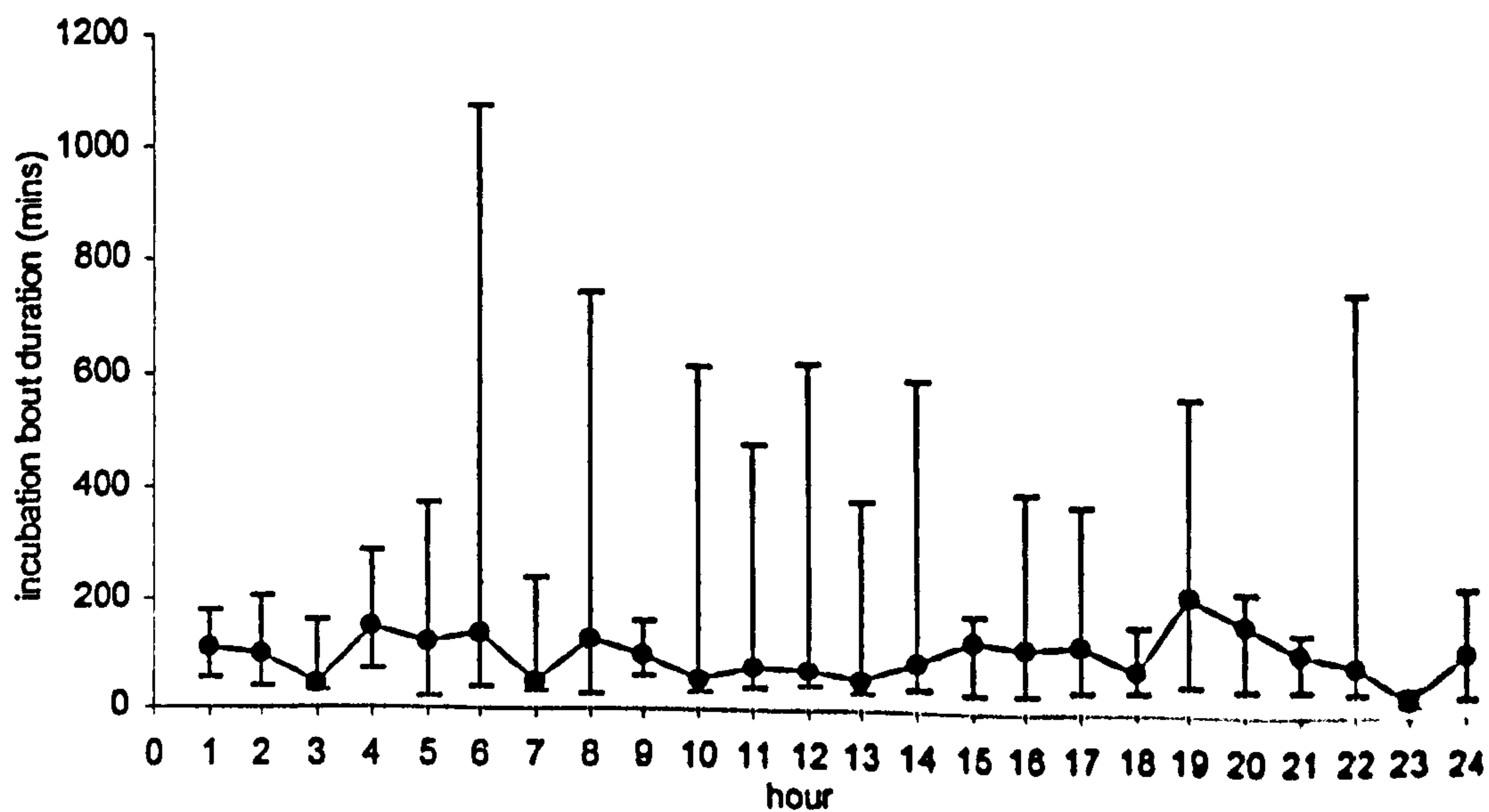


Figure 15. Incubation bout duration for biparental nests with time of day (medians  $\pm$  range were calculated from the median daily values from seven or eight nests for each hour of the day).

*Trip frequency*

Trip frequency varied with time of day for uniparental nests (GLM on log transformed nest-means: hour  $F_{23,849}=39.330$ ,  $P<0.001$ , partial  $R^2=0.516$ ; nest  $F_{37,849}=11.369$ ,  $P<0.001$ , partial  $R^2=0.331$ ; model  $R^2_{adj}=0.583$ , Fig. 16).

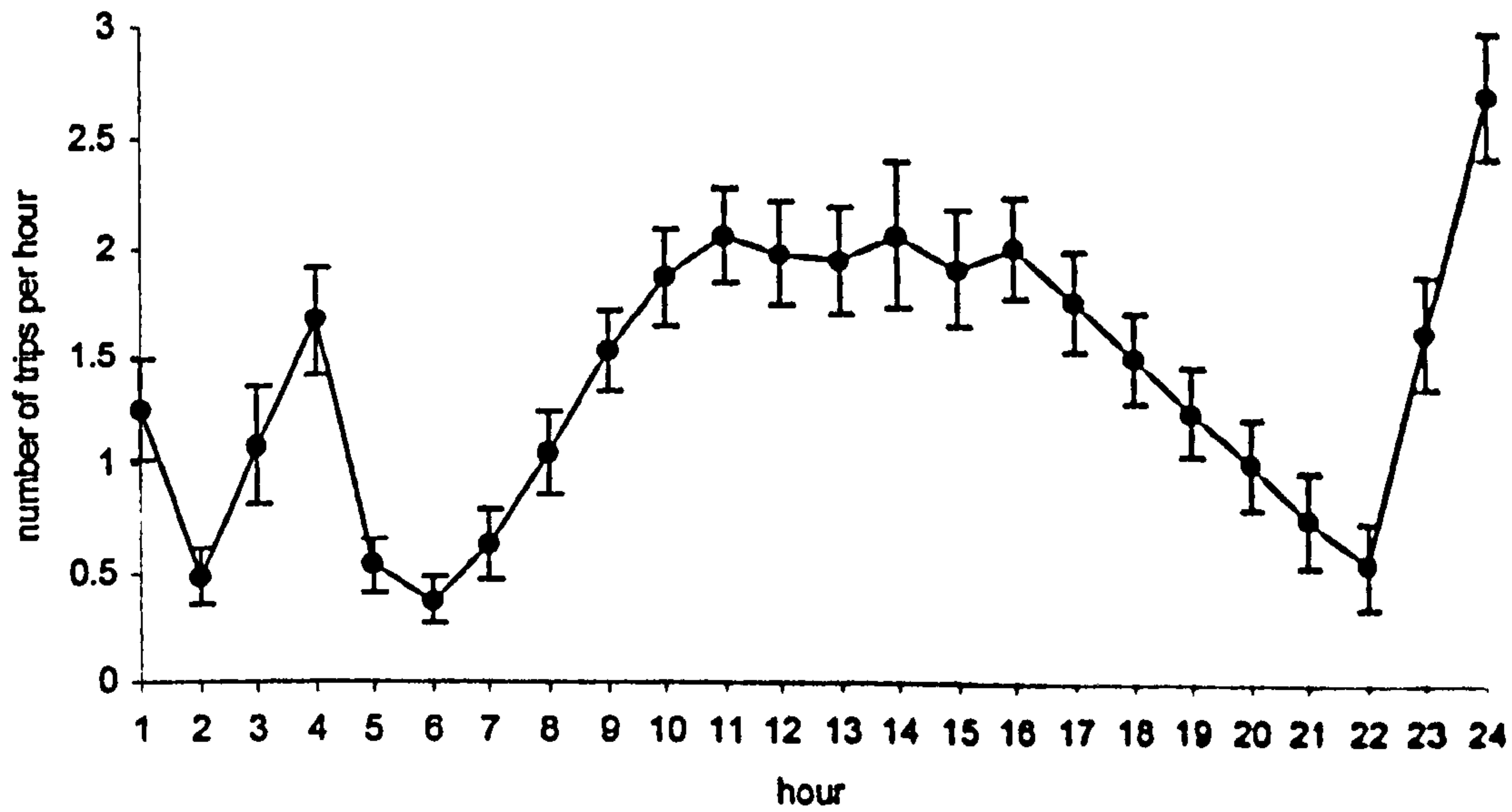


Figure 16. Trip frequency with time of day at uniparental nests (mean ± 95% c.i. of nest means, 34 or 35 nests used to calculate each mean).

Trip frequency varied with time of day for biparental nests (GLM on log transformed nest-means: hour  $F_{23,161}=6.572$ ,  $P<0.001$ , partial  $R^2=0.484$ ; nest  $F_{7,161}=17.524$ ,  $P<0.001$ , partial  $R^2=0.432$ ; model  $R^2_{adj}=0.561$ , Fig. 17).

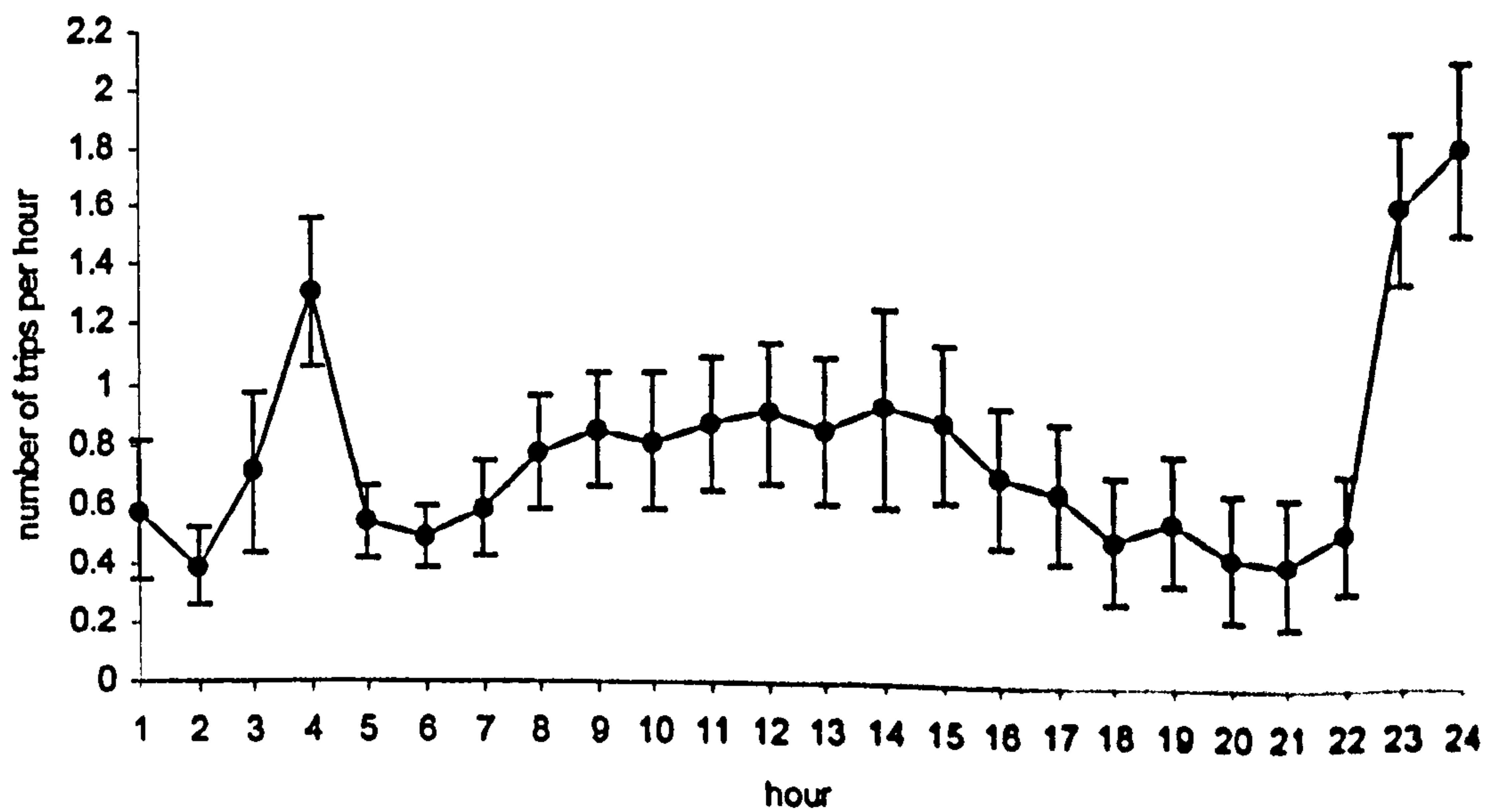


Figure 17. Trip frequency with time of day at biparental nests (mean ± 95% c.i. of nest means, eight nests used to calculate each mean).

### Proportion of time eggs below 20°C

The proportion of time that eggs of both uniparental and biparental nests spent below 20°C varied significantly with time of day (GLM: uniparental  $F_{23,888}=8.434$ ,  $P<0.001$ ,  $R^2_{\text{adj}}=0.158$ ; biparental  $F_{23,168}=1.742$ ,  $P=0.025$ ,  $R^2_{\text{adj}}=0.082$ , both analyses balanced with a case from all 38 and eight uniparental and biparental nests, respectively, in each hour). The proportion of time that eggs of uniparental nests spent below 20°C appeared highest in the middle of the day, at dawn and around midnight, but the pattern for biparental nests was less clear (Figs. 18 & 19).

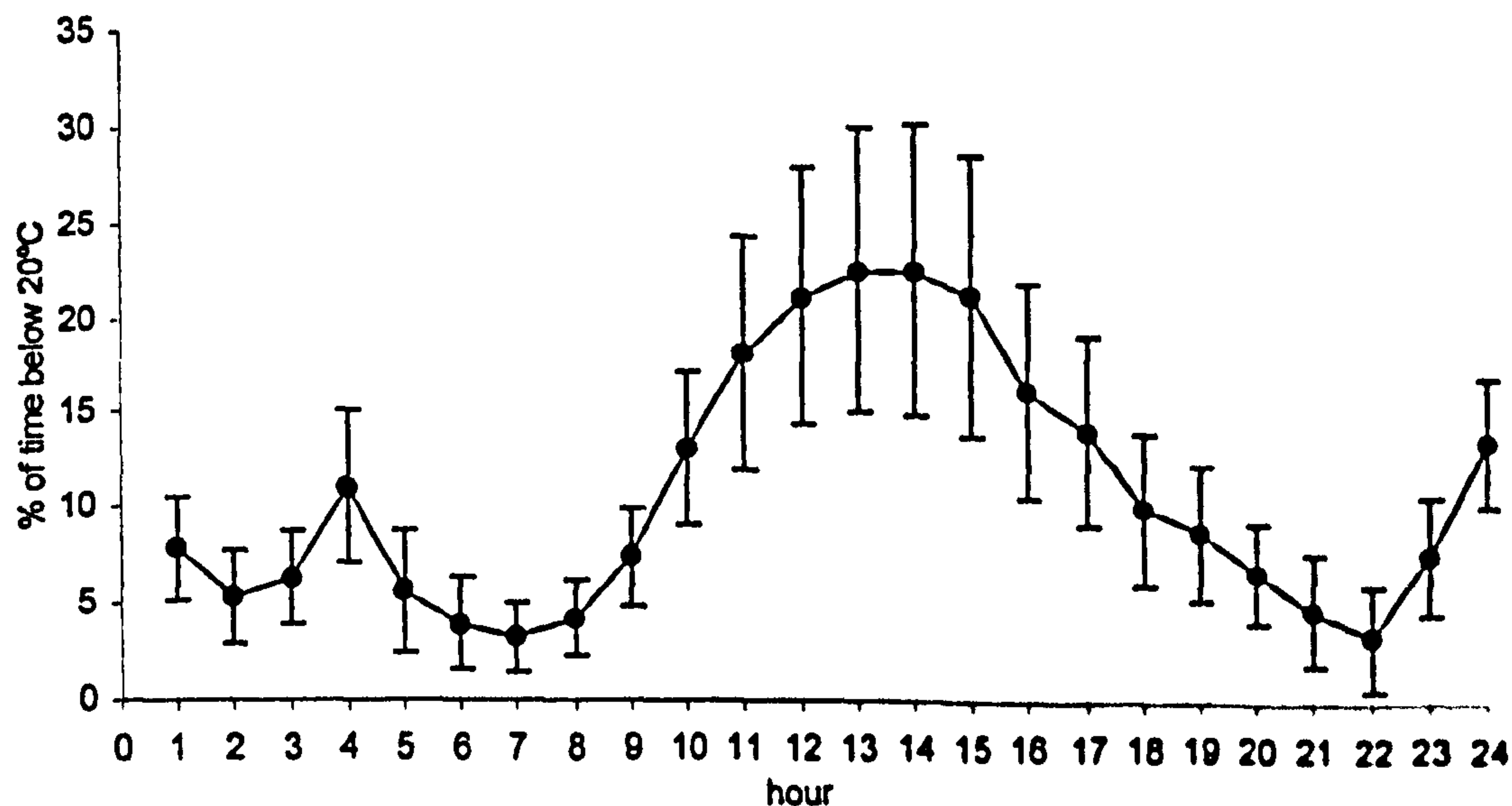


Figure 18. The proportion of time that eggs of uniparental nests spent below 20°C with time of day (means  $\pm$  95% c.i., 38 nests each contributed one datum to each hour).

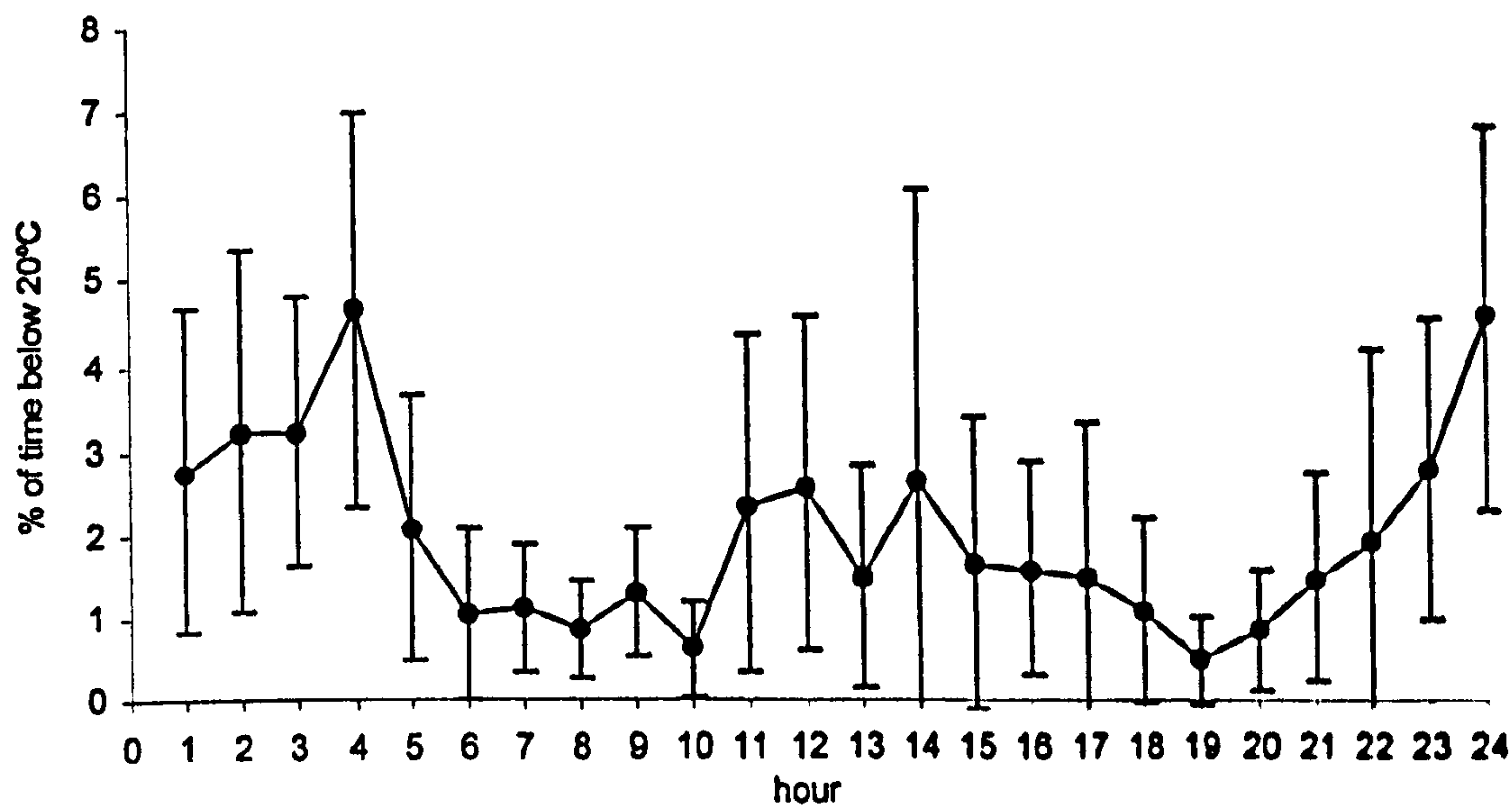


Figure 19. The proportion of time that eggs of biparental nests spent below 20°C with time of day (means  $\pm$  95% c.i., eight nests each contributed one datum to each hour).

#### *Incidence of egg neglect*

The median number of periods of egg neglect (trips of more than 2 hours, Chapter 4) initiated per hour varied significantly with time of day in uniparental nests but not in biparental nests (Kruskal Wallis testing whether the mean number of bouts of egg initiated varied with the hour of the day, uniparental:  $\chi^2_{23}=121.665$ ,  $P<0.001$  ; biparental:  $\chi^2_{23}=22.116$ ,  $P=0.513$ , both tests balanced with 38 uniparental and eight biparental nests each contributing a datum to each hour category). Bouts of egg neglect appeared to start most frequently from mid-morning to early afternoon (Fig. 20).

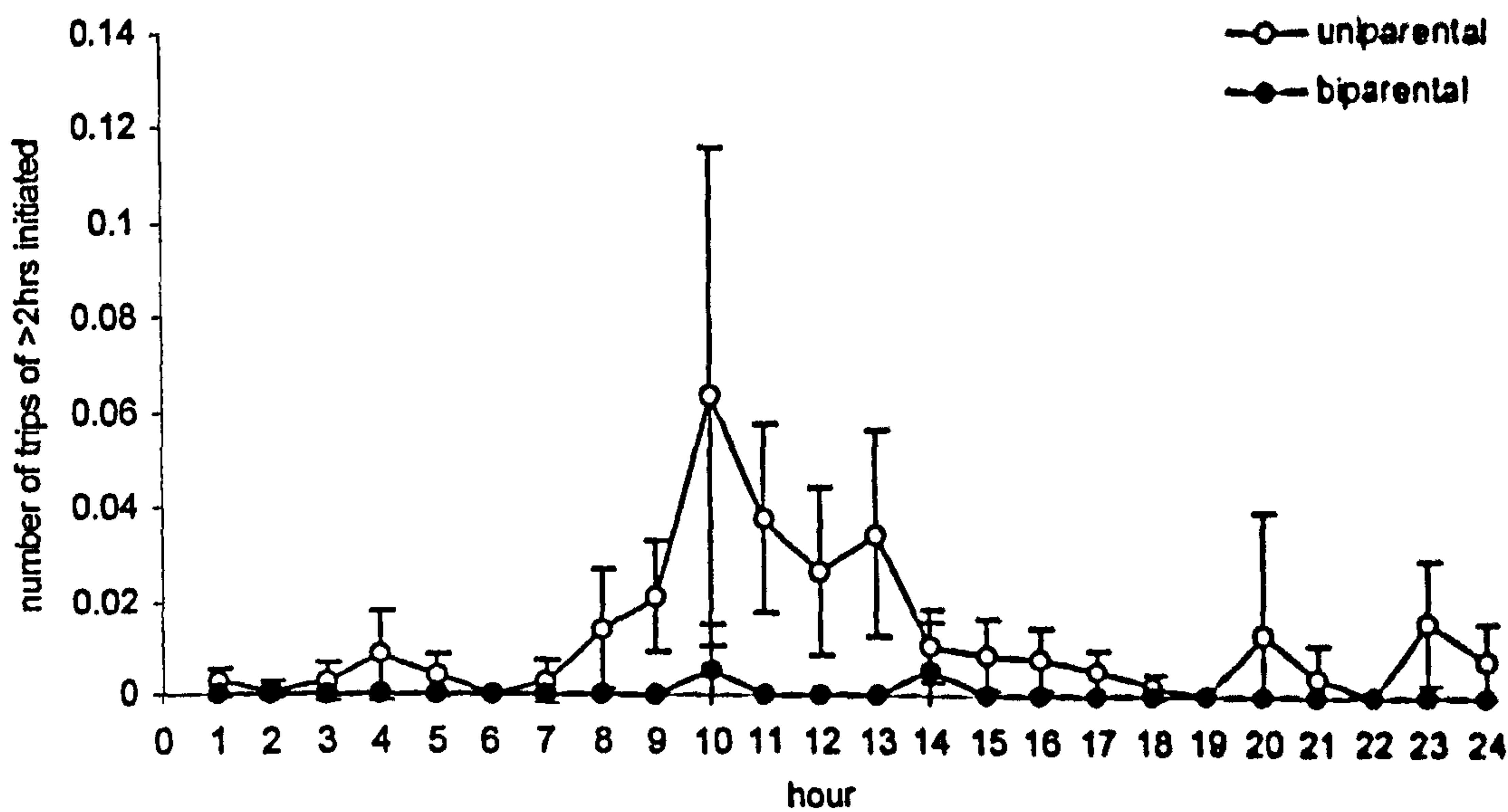


Figure 20. The number of trips of more than two hours initiated with time of day (although the data were not normally distributed the means of nest medians are plotted as the medians of nest medians were all zero and so could not illustrate the pattern of variation).

#### *Power for incubation*

The estimated power for incubation of both uniparental and biparental nests varied significantly with time of day (GLM: uniparental  $F_{23,888}=7.667$ ,  $P<0.001$ ,  $R^2_{adj}=0.144$ ; biparental  $F_{23,168}=3.792$ ,  $P<0.001$ ,  $R^2_{adj}=0.252$ , both analyses balanced with a case from all 38 and eight uniparental and biparental nests, respectively, in each hour, Figs. 21 & 22).

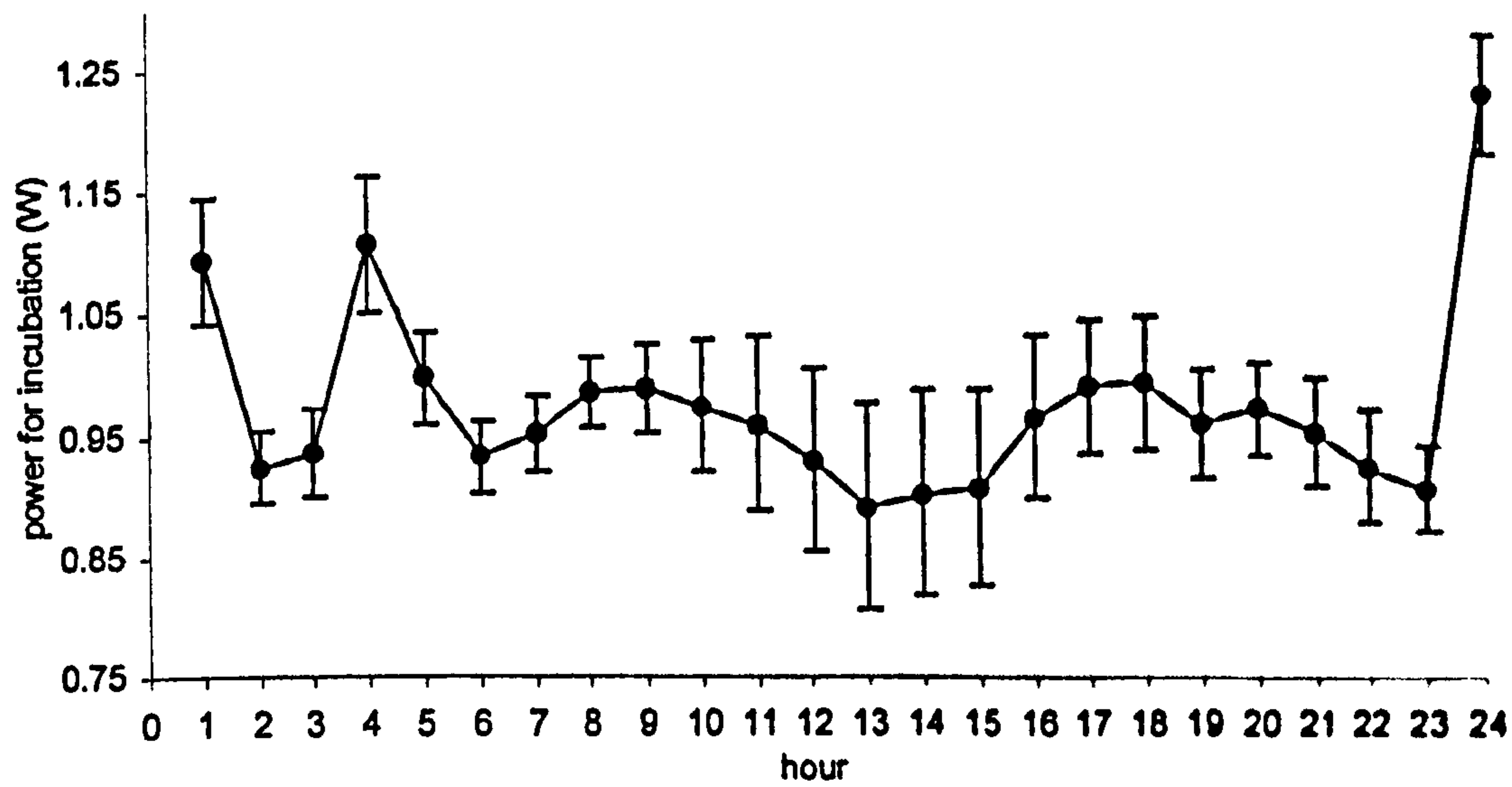


Figure 21. The power for incubation for uniparental nests with time of day (means  $\pm$  95% c.i., 38 nests each contributed one datum to each hour).

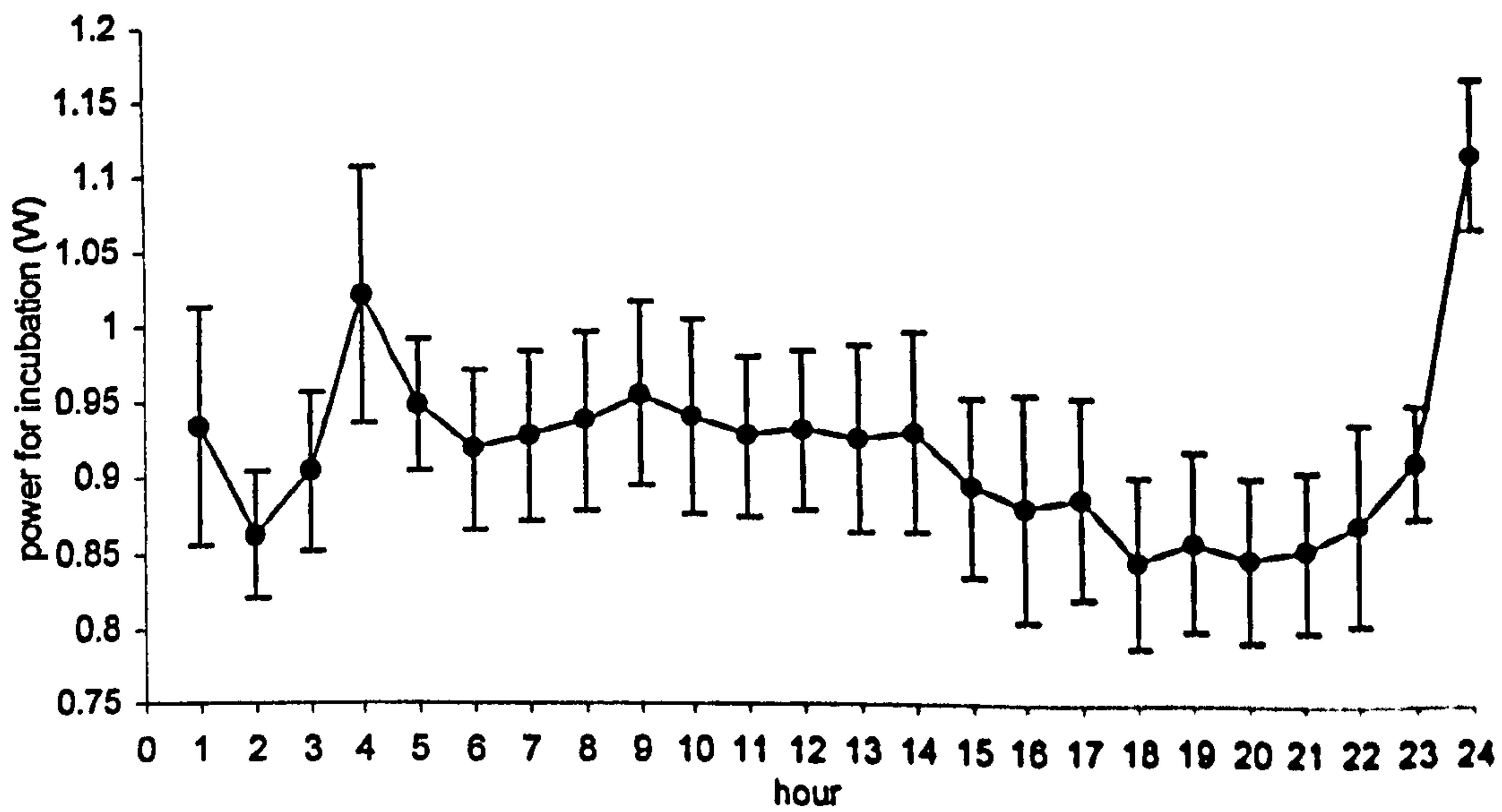


Figure 22. The power for incubation for biparental nests with time of day (means  $\pm$  95% c.i., eight nests each contributed one datum to each hour).



## **Daylight and darkness**

### *Nest attendance*

Uniparental dotterel attended the nest a significantly greater proportion of time during darkness (darkness was defined as from sunset to sunrise) than during daylight (Paired t-test comparing within nests:  $t_{37}=2.890$ ,  $P=0.006$ , nests were attended a  $0.049 \pm 0.035$  greater proportion of time during darkness).

Biparental dotterel attended the nest a significantly smaller proportion of time during darkness than during daylight (Paired t-test comparing within nests:  $t_7=3.317$ ,  $P=0.013$ , nests were attended a  $0.039 \pm 0.028$  smaller proportion of time during darkness).

### *Trip duration*

Trips away from the nest were significantly shorter during darkness than during daylight at uniparental nests (Paired t-test comparing within nests:  $t_{37}=2.115$ ,  $P=0.041$ , trips were  $1.3 \pm 1.2$  mins longer during daylight; the nest medians of daily medians used in the analysis were not distributed significantly non-normally).

At biparental nests, trip duration did not differ significantly between darkness and daylight (Paired t-test comparing within nests:  $t_7=0.812$ ,  $P=0.443$ , trips were  $0.9 \pm 2.8$  mins longer during darkness).

### *Incubation bout duration*

Incubation bouts were significantly longer during darkness than during daylight at uniparental nests (Paired t-test comparing within nests:  $t_{37}=2.684$ ,  $P=0.011$ , bouts were  $27.7 \pm 20.9$  mins longer during darkness; the nest medians of daily medians used in the analysis were not significantly non-normally distributed).

At biparental nests, incubation bouts duration did not significantly differ between daylight and darkness (Paired t-test comparing within nests:  $t_7=0.345$ ,  $P=0.741$ , bouts were  $18.8 \pm 129.0$  mins shorter during darkness).

### *Trip frequency*

Trip frequency did not differ between daylight and darkness in uniparental dotterel (Paired t-test comparing within nests:  $t_{37}=0.272$ ,  $P=0.787$ , trips were  $0.017 \pm 0.124 \text{ hr}^{-1}$  more frequent during darkness).

At biparental nests, the frequency of trips from the nest did not differ between daylight and darkness (Paired t-test comparing within nests:  $t_7=1.82$ ,  $P=0.112$ , trips were  $0.172 \pm 0.224 \text{ hr}^{-1}$  more frequent during darkness).

### *Proportion of time eggs below 20°C*

Eggs did not spend a significantly different proportion of time below 20°C during daylight and darkness at uniparental nests (Paired t-test comparing within nests:  $t_{37}=1.941$ ,  $P=0.060$ , eggs spent  $0.034 \pm 0.035$  smaller proportion of the time below 20°C during darkness).

At biparental nest, eggs spent a significantly greater proportion of time below 20°C during darkness than during daylight (Paired t-test comparing within nests:  $t_7=2.836$ ,  $P=0.025$ , eggs spent  $0.021 \pm 0.017$  greater proportion of the time below 20°C during darkness).

### *Incidence of egg neglect*

Eggs were neglected at a significantly higher rate during daylight than during darkness at uniparental nests (Wilcoxon matched pairs test comparing within nests:  $Z=2.744$ ,  $N=38$ ,  $P=0.006$ , eggs were neglected  $0.006$  ( $\pm 95\%$  c.i.  $0.000 - 0.014$ ) more times per hour in the light).

At biparental nests, there was no significant difference in the frequency of egg neglect between day and night (Wilcoxon matched pairs test comparing within nests:  $Z=1.342$ ,

$N=8$ ,  $P=0.180$ , eggs were neglected  $0.000 (\pm 95\% \text{ c.l. } 0.000 - 0.003)$  more times per hour during darkness).

There was no evidence of high rates of nocturnal egg neglect at the beginning of incubation for uniparental nests (although there was only sufficient data to examine this from four days after the first egg was laid, which typically corresponds to one day after clutch completion, Fig. 23).

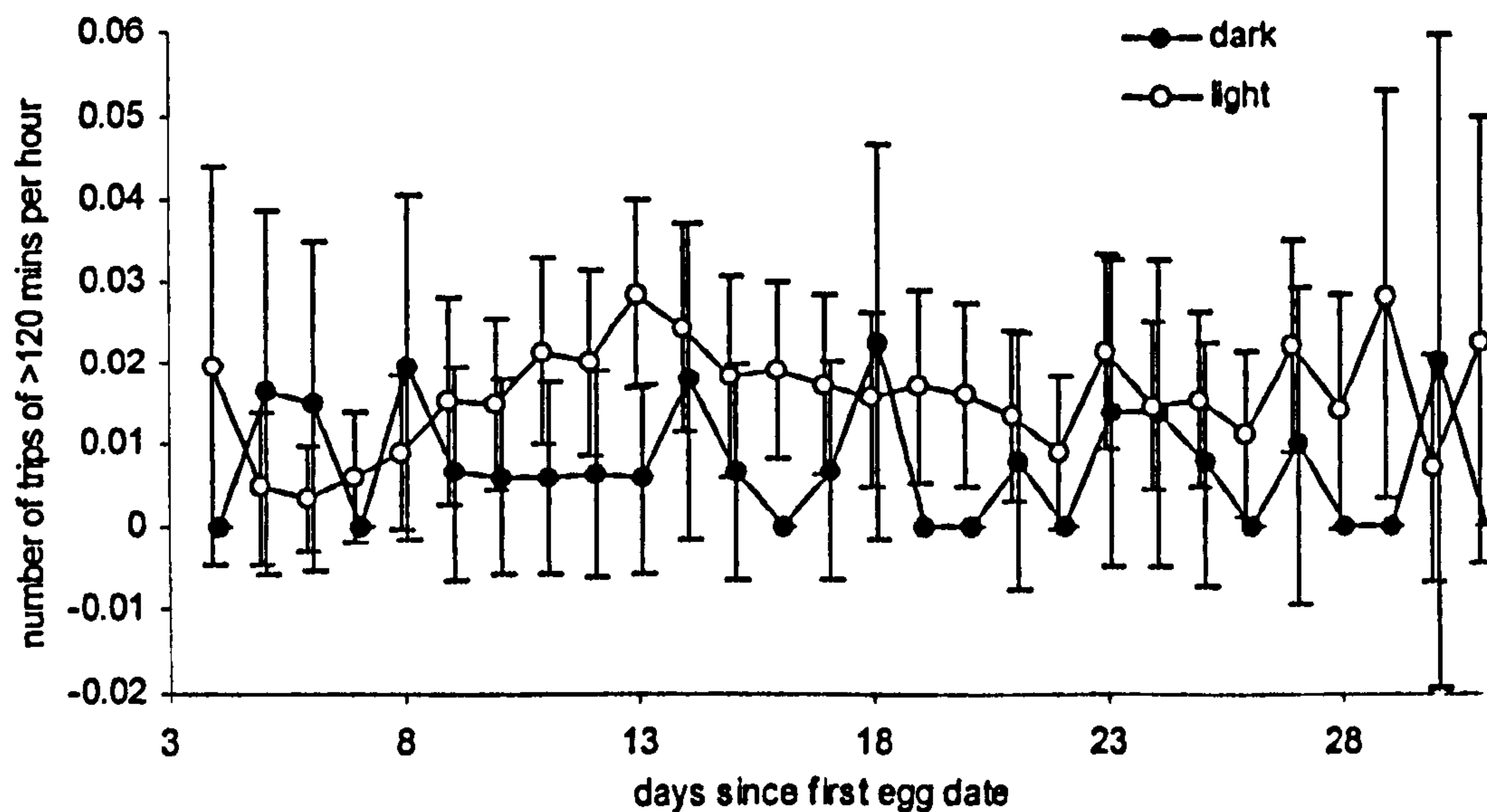


Figure 23. The rate of egg neglect at uniparental nests with light and days since first egg date (twilight was classed as dark, points are offset slightly to allow confidence limits for both classes to be seen; between five and 26 nests used to calculate each mean).

#### *Power for incubation*

Uniparental dotterel expended significantly more power on incubation during darkness than during daylight (Paired t-test comparing within nests:  $t_{37}=3.594$ ,  $P<0.001$ ,  $0.087 \pm 0.049$  W more power expended during darkness).

Biparental dotterel expended significantly more power on incubation during darkness than during daylight (Paired t-test comparing within nests:  $t_7=2.815$ ,  $P=0.026$ ,  $0.062 \pm 0.052$  W more power expended during darkness).

Both uniparental and biparental dotterel used more power to incubate at night. This difference was not due to higher steady state incubation costs as the power for steady state incubation did not significantly differ between daylight and darkness at uniparental nests and was significantly lower in darkness than daylight at biparental nests (Paired t-test comparing within nests: uniparental  $t_{37}=0.305$ ,  $P=0.762$ ,  $0.001 \pm 0.005$  W less power expended during darkness; biparental  $t_7=6.815$ ,  $P<0.001$ ,  $0.008 \pm 0.003$  W less power expended during darkness). Egg cooling rate was significantly higher during darkness, which will have increased the energetic cost of rewarming eggs (Paired t-test comparing within nests: uniparental  $t_{37}=11.416$ ,  $P<0.001$ ,  $0.0186 \pm 0.0033$  greater temperature drop in the first five seconds of inattendant during darkness; biparental  $t_7=9.704$ ,  $P<0.001$ ,  $0.0182 \pm 0.0044$  greater temperature drop in the first five seconds of inattendant during darkness). The higher cooling rate during darkness is the only explanation for higher costs of incubation during darkness that is common to both uniparental and biparental nests. Lower attendance can increase the cost of incubation (Chapter 3) but cannot be a complete explanation for the differences in incubation costs between daylight and darkness as, although attendance is lower during darkness than daylight at uniparental nests, the reverse is true at biparental nests. At uniparental nests trips were more frequent during daylight, which can increase costs, but daylight trips were longer, which can reduce costs (Chapter 3). As the index of the energetic cost of thermoregulation is higher during darkness, dotterel have to bear both increased energetic costs of incubation and thermoregulation during darkness (Paired t-test comparing the cost of thermoregulation within nests: uniparental  $t_{37}=11.144$ ,  $P<0.001$ ,  $0.394 \pm 0.072$  W more expended during darkness; biparental  $t_7=7.115$ ,  $P<0.001$ ,  $0.369 \pm 0.123$  W more expended during darkness).

## Egg cooling rate

### Nest attendance

Nest attendance did not vary significantly with the potential cooling rate of egg if unattended at uniparental nests (GLM: cooling rate  $F_{1,227}=0.969$ ,  $P=0.326$ , partial  $R^2=0.004$ ,  $\beta=0.110 \pm 0.220$ , nest identity  $F_{37,227}=6.052$ ,  $P<0.001$ , partial  $R^2=0.497$ , model  $R^2_{adj}=0.414$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 24).

Nest attendance increased significantly with cooling rate at biparental nests (GLM: cooling rate  $F_{1,63}=18.223$ ,  $P<0.001$ , partial  $R^2=0.224$ ,  $\beta=0.279 \pm 0.130$ , nest identity  $F_{7,63}=4.768$ ,  $P<0.001$ , partial  $R^2=0.346$ , model  $R^2_{adj}=0.380$ , the range of cooling rates was confined to  $\geq 0.08^\circ\text{C}$  to  $\leq 0.24^\circ\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 24).

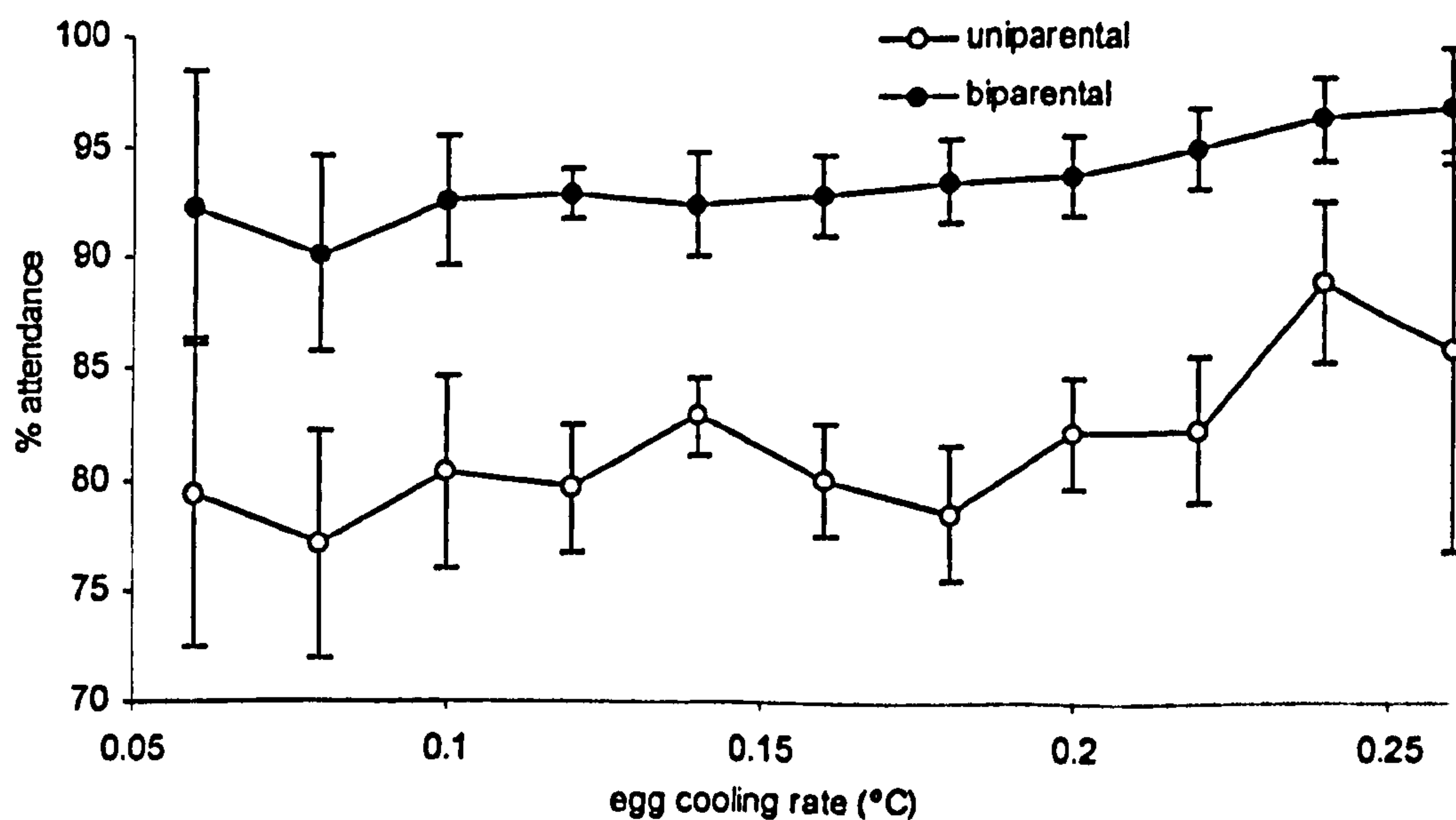


Figure 24. Nest attendance with egg cooling rate (temperature change  $^\circ\text{C}$  per 5s) and parental care (means  $\pm$  95% c.i., between six and eight biparental nests and 31 and 38 uniparental nests used to calculate each mean).

### Trip duration

The trip durations of uniparental nests did not vary significantly with cooling rate (GLM: cooling rate  $F_{1,221}=3.630$ ,  $P=0.058$ , partial  $R^2=0.016$ ,  $\beta=26.14 \pm 27.04$ , nest identity

$F_{37,221}=1.687$ ,  $P=0.012$ , partial  $R^2=0.220$ , model  $R^2_{\text{adj}}=0.098$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  to improve the balance of the GLM so that cooling rate classes each included a datum from  $97.8\% \pm 1.5\%$  of 38 nests, Fig. 25).

The trip durations of biparental nests did not vary significantly with cooling rate (GLM: cooling rate  $F_{1,61}=1.587$ ,  $P=0.213$ , partial  $R^2=0.025$ ,  $\beta=-5.42 \pm 8.60$ , nest identity  $F_{7,61}=4.403$ ,  $P=0.001$ , partial  $R^2=0.336$ , model  $R^2_{\text{adj}}=0.266$ , the range of cooling rates was confined to  $\geq 0.08^\circ\text{C}$  to  $\leq 0.24^\circ\text{C}$  to improve the balance of the GLM so that cooling rate classes each included a datum from  $97.2\% \pm 3.6\%$  of eight nests, Fig. 25).

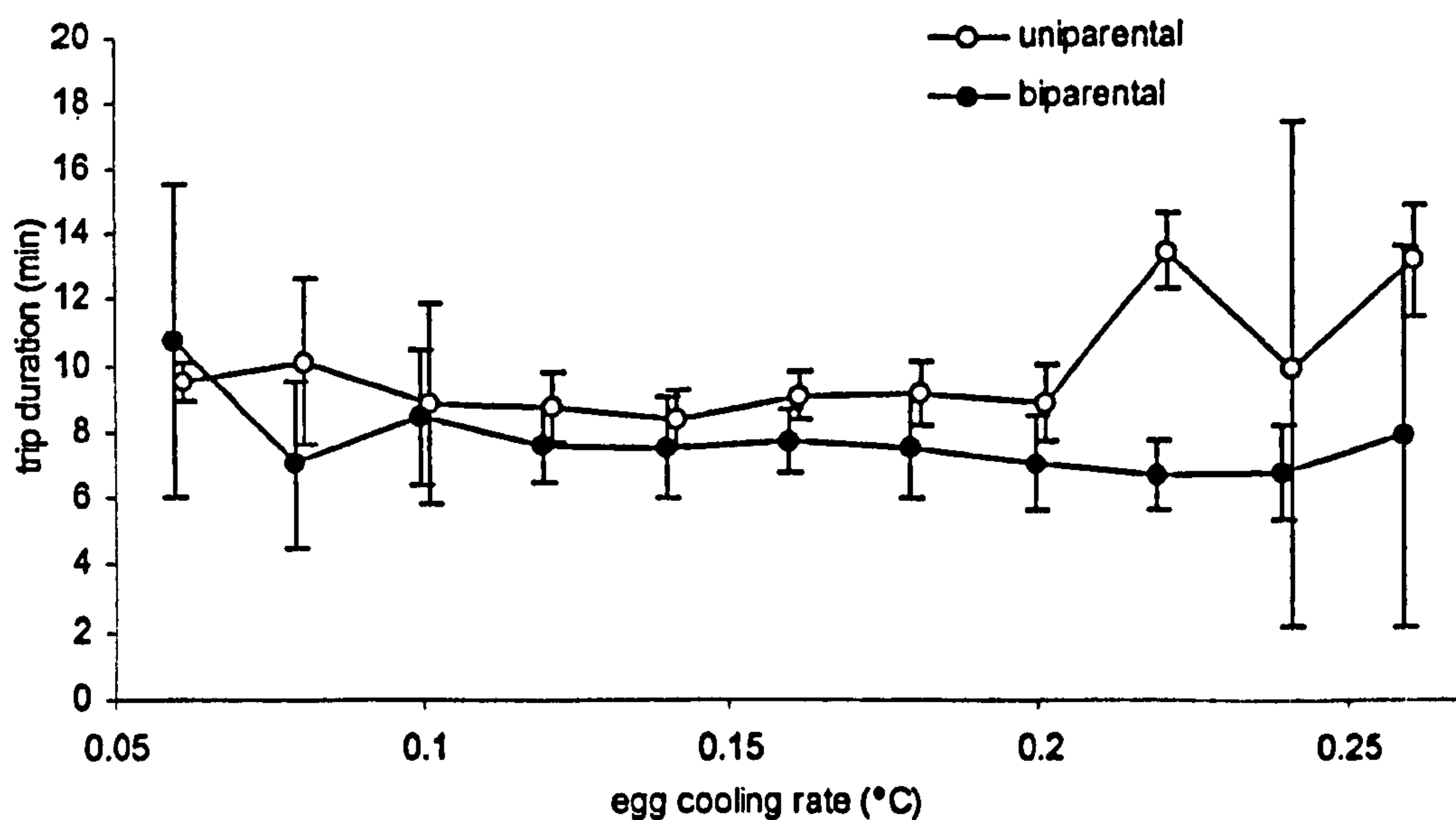


Figure 25. Trip duration with egg cooling rate and parental care (means  $\pm$  95% c.i., points offset slightly to allow error bars to be seen, between five and eight biparental nests and 17 and 38 uniparental nests used to calculate each mean).

#### *Incubation bout duration*

The incubation bout durations of uniparental nests increased significantly with cooling rate (GLM: cooling rate  $F_{1,219}=13.214$ ,  $P<0.001$ , partial  $R^2=0.430$ ,  $\beta=161.8 \pm 87.7$ , nest identity  $F_{37,219}=4.469$ ,  $P<0.001$ , partial  $R^2=0.057$ , model  $R^2_{\text{adj}}=0.357$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  to improve the balance of the GLM so that cooling rate classes each included a datum from  $97.0\% \pm 2.9\%$  of 38 nests, Fig. 26).

The incubation bout durations of biparental nests did not vary significantly with cooling rate (GLM: cooling rate  $F_{1,61}=2.621$ ,  $P=0.111$ , partial  $R^2=0.041$ ,  $\beta=347.6 \pm 429.3$ , nest identity  $F_{7,61}=2.315$ ,  $P=0.037$ , partial  $R^2=0.210$ , model  $R^2_{adj}=0.133$ , the range of cooling rates was confined to  $\geq 0.08^\circ\text{C}$  to  $\leq 0.24^\circ\text{C}$  to improve the balance of the GLM so that cooling rate classes each included a datum from  $97.2\% \pm 3.6\%$  of eight nests, Fig. 26).

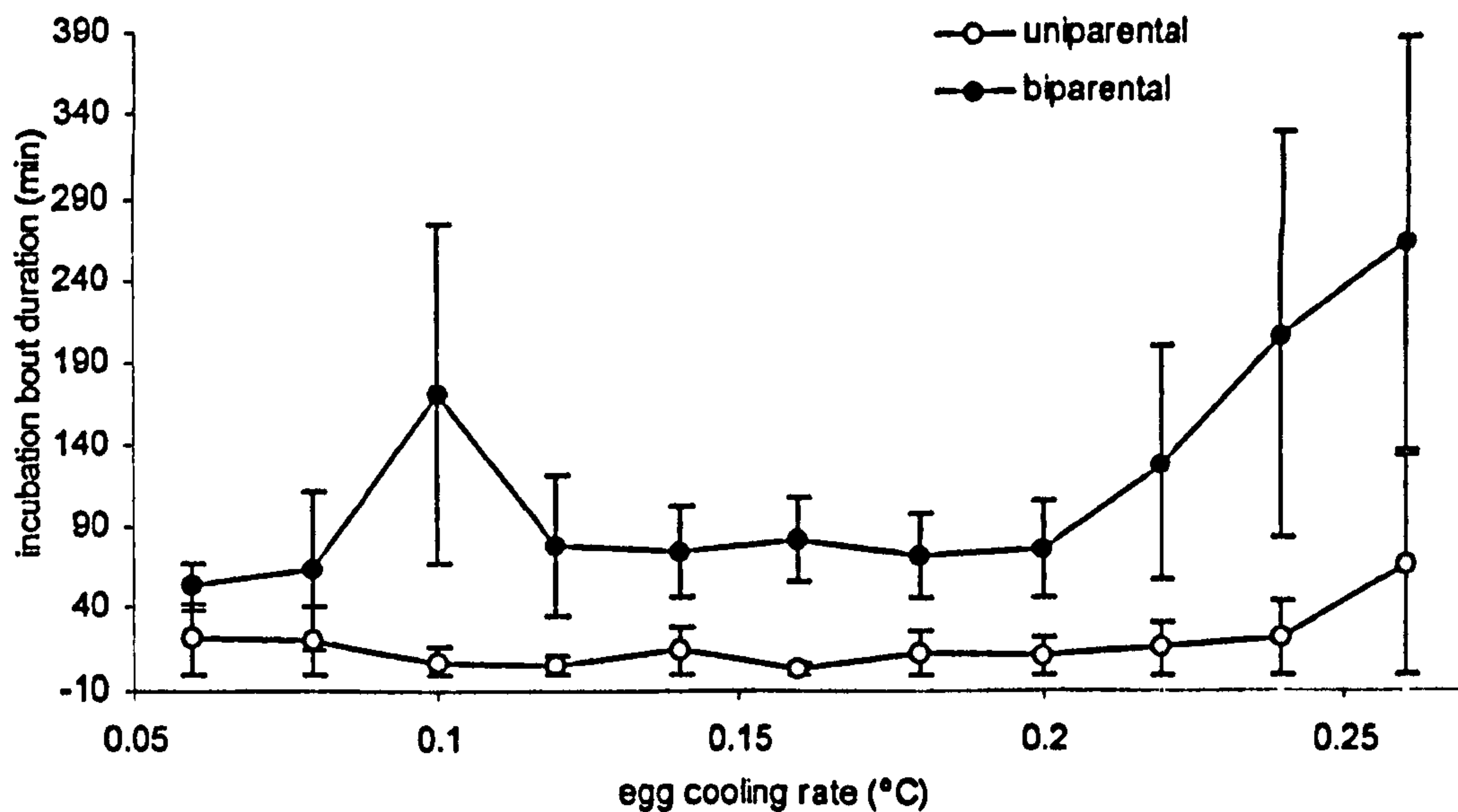


Figure 26. Incubation bout duration with egg cooling rate and parental care (means  $\pm$  95% c.i., between five and eight biparental nests and 14 and 38 uniparental nests used to calculate each mean).

### *Trip frequency*

Trip frequency decreased significantly with cooling rate at uniparental nests (GLM: cooling rate  $F_{1,227}=46.622$ ,  $P<0.001$ , partial  $R^2=0.170$ ,  $\beta=-4.786 \pm 0.179$ , nest identity  $F_{37,227}=2.458$ ,  $P<0.001$ , partial  $R^2=0.286$ , model  $R^2_{adj}=0.273$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 27).

Trip frequency also decreased significantly with cooling rate at biparental nests (GLM: cooling rate  $F_{1,63}=14.385$ ,  $P<0.001$ , partial  $R^2=0.186$ ,  $\beta=-2.002 \pm 1.055$ , nest identity  $F_{7,63}=3.678$ ,  $P=0.002$ , partial  $R^2=0.290$ , model  $R^2_{adj}=0.312$ , the range of cooling rates was confined to

$\geq 0.08^{\circ}\text{C}$  to  $\leq 0.24^{\circ}\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 27).

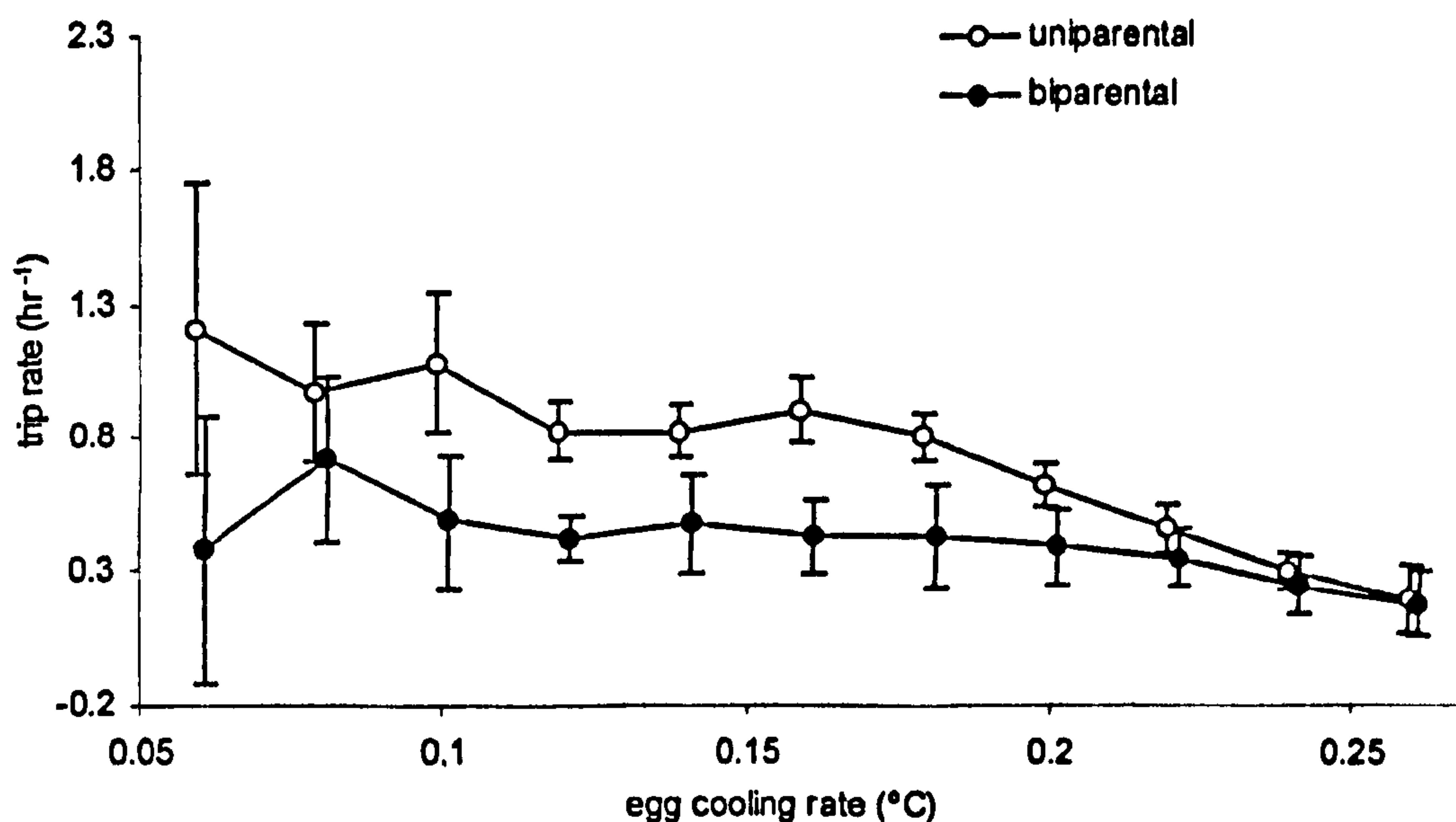


Figure 27. Trip frequency with egg cooling rate and parental care (means  $\pm$  95% c.i., points offset slightly to allow error bars to be seen, between six and eight biparental nests and 31 and 38 uniparental nests used to calculate each mean).

#### *Proportion of time eggs below 20°C*

The proportion of time that eggs of uniparental nests spent below 20°C increased significantly with cooling rate (GLM: cooling rate  $F_{1,227}=45.497$ ,  $P<0.001$ , partial  $R^2=0.167$ ,  $\beta=0.682 \pm 0.199$ , nest identity  $F_{37,227}=9.457$ ,  $P<0.001$ , partial  $R^2=0.607$ , model  $R^2_{adj}=0.574$ , the range of cooling rates was confined to  $\geq 0.1^{\circ}\text{C}$  to  $\leq 0.22^{\circ}\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 28).

The proportion of time that eggs of biparental nests spent below 20°C also increased significantly with cooling rate (GLM: cooling rate  $F_{1,83}=19.689$ ,  $P<0.001$ , partial  $R^2=0.238$ ,  $\beta=0.138 \pm 0.062$ , nest identity  $F_{7,83}=3.136$ ,  $P=0.007$ , partial  $R^2=0.258$ , model  $R^2_{adj}=0.321$ , the range of cooling rates was confined to  $\geq 0.08^{\circ}\text{C}$  to  $\leq 0.24^{\circ}\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 28). The coefficients for the cooling rates differed significantly between parental care systems so that the proportion of



time the eggs of uniparental nests spent below 20°C increased faster with egg cooling rate in uniparental nests (Fig. 28).

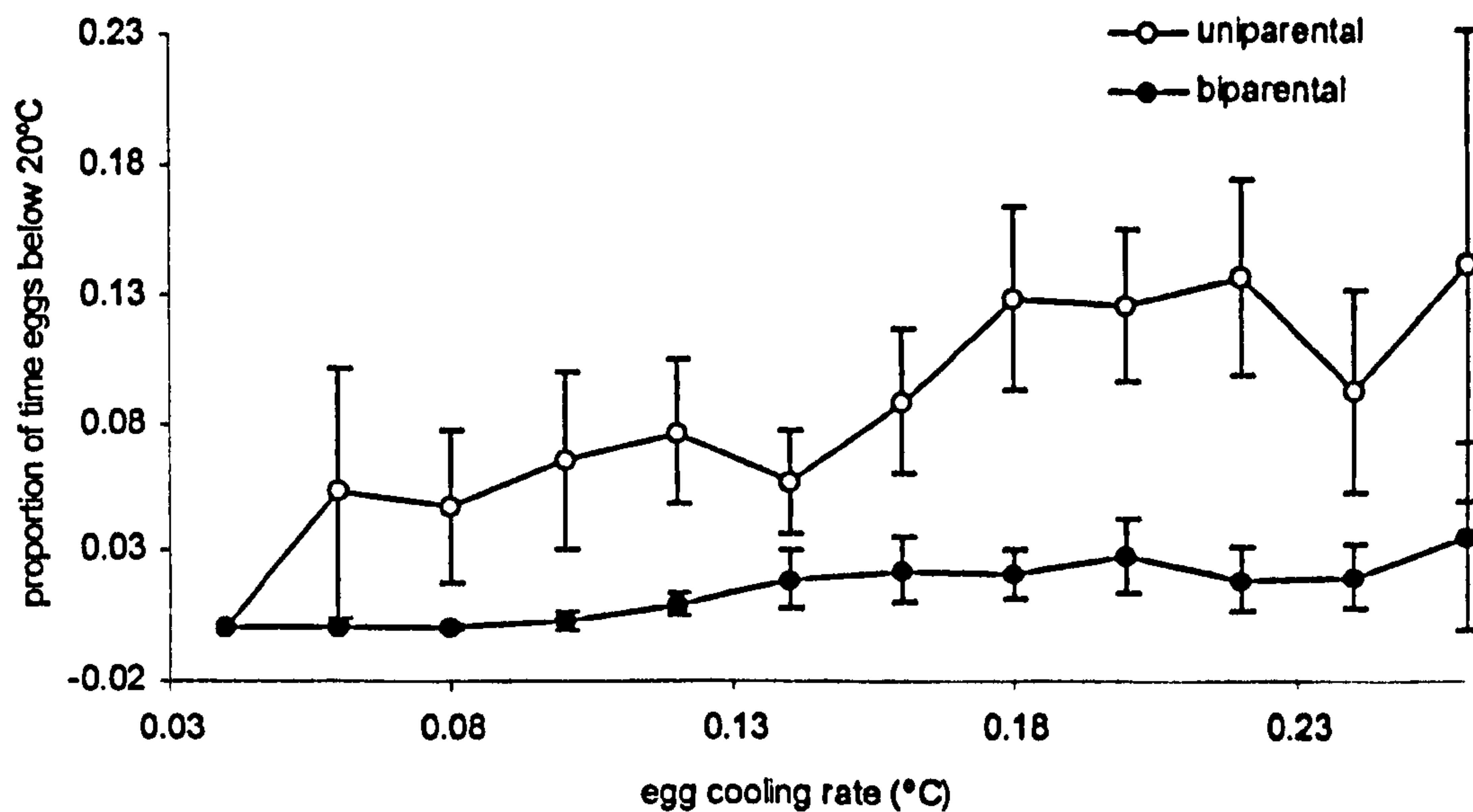


Figure 28. The estimated proportion of time that eggs spent below 20°C with egg cooling rate and parental care (means  $\pm$  95% c.i., between six and eight biparental nests and 16 and 38 uniparental nests used to calculate each mean).

#### *Incidence of egg neglect*

The rate of egg neglect increased significantly with egg cooling rate in uniparental nests (Spearman's rank correlation:  $r_s=0.964$ ,  $N=7$ ,  $P<0.001$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  in  $0.2^\circ\text{C}$  increments so that each nest could contribute a datum to the mean calculated for each cooling rate class, Fig. 29). Although the rate of neglect increased within the range of cooling rate values tested, it may have then decreased at cooling rates above this range (Fig. 29).

The rate of egg neglect was not associated significantly with egg cooling rate in biparental nests (Spearman's rank correlation:  $r_s=0.274$ ,  $N=9$ ,  $P=0.476$ , the range of cooling rates was confined to  $\geq 0.08^\circ\text{C}$  to  $\leq 0.24^\circ\text{C}$  in  $0.2^\circ\text{C}$  increments so that each nest could contribute a datum to the mean calculated for each cooling rate class, Fig. 29).

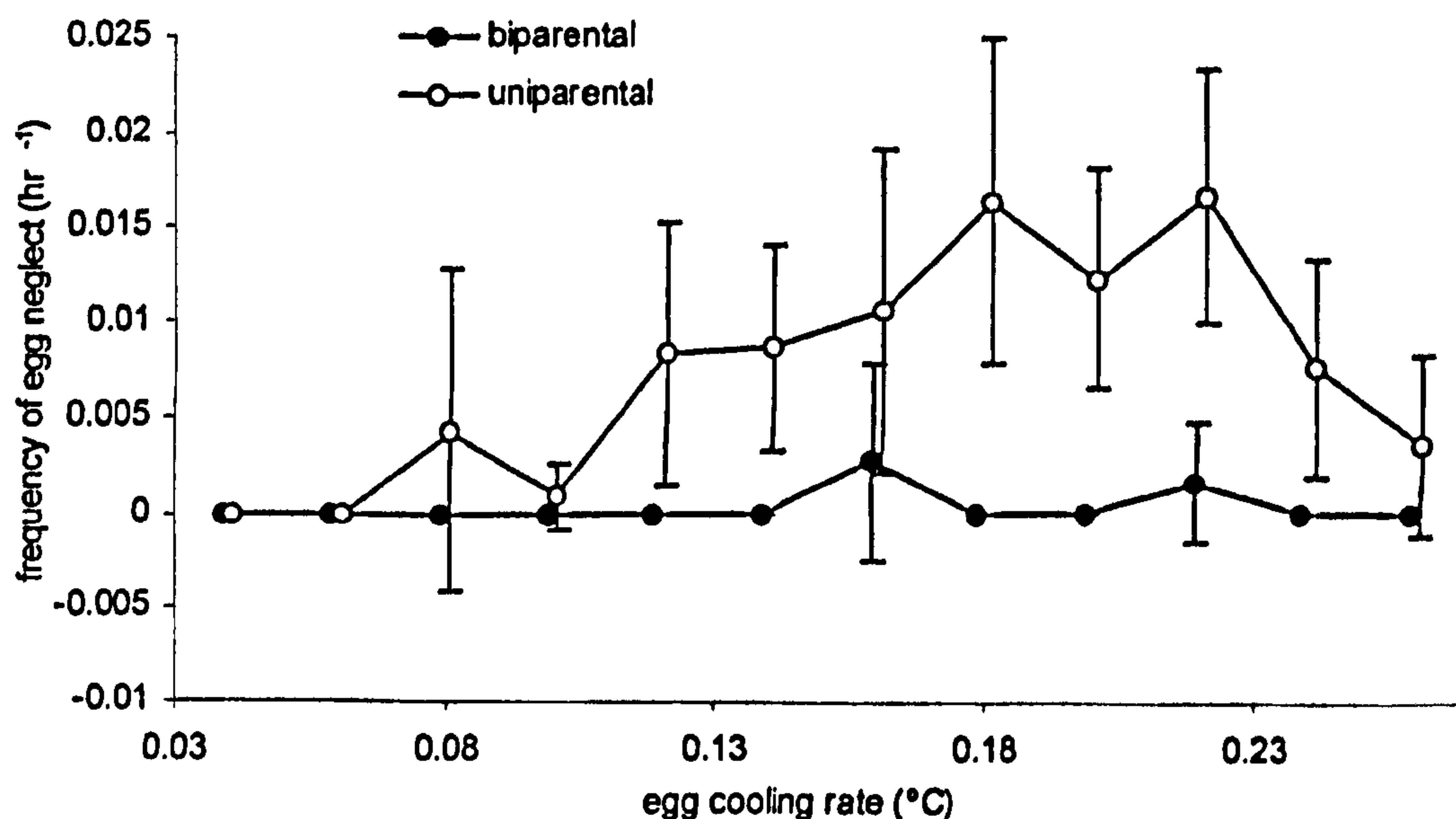


Figure 29. The frequency of egg neglect with egg cooling rate and parental care (means  $\pm$  95% c.i. , points offset slightly to allow error bars to be seen, between six and eight biparental nests and 16 and 38 uniparental nests used to calculate each mean).

#### *Power for incubation*

The power expended on incubation did not vary significantly with cooling rate at uniparental nests (GLM: cooling rate  $F_{1,227}=0.372$ ,  $P=0.542$ , partial  $R^2=0.002$ ,  $\beta=0.090 \pm 0.290$ , nest identity  $F_{37,227}=5.010$ ,  $P<0.001$ , partial  $R^2=0.450$ , model  $R^2_{adj}=0.358$ , the range of cooling rates was confined to  $\geq 0.1^\circ\text{C}$  to  $\leq 0.22^\circ\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 30).

The power expended on incubation increased significantly with cooling rate at biparental nests (GLM: cooling rate  $F_{1,63}=55.766$ ,  $P<0.001$ , partial  $R^2=0.470$ ,  $\beta=0.658 \pm 0.176$ , nest identity  $F_{7,63}=28.072$ ,  $P<0.001$ , partial  $R^2=0.757$ , model  $R^2_{adj}=0.775$ , the range of cooling rates was confined to  $\geq 0.08^\circ\text{C}$  to  $\leq 0.24^\circ\text{C}$  to ensure the GLM was balanced with one datum per nest per cooling rate class, Fig. 30).

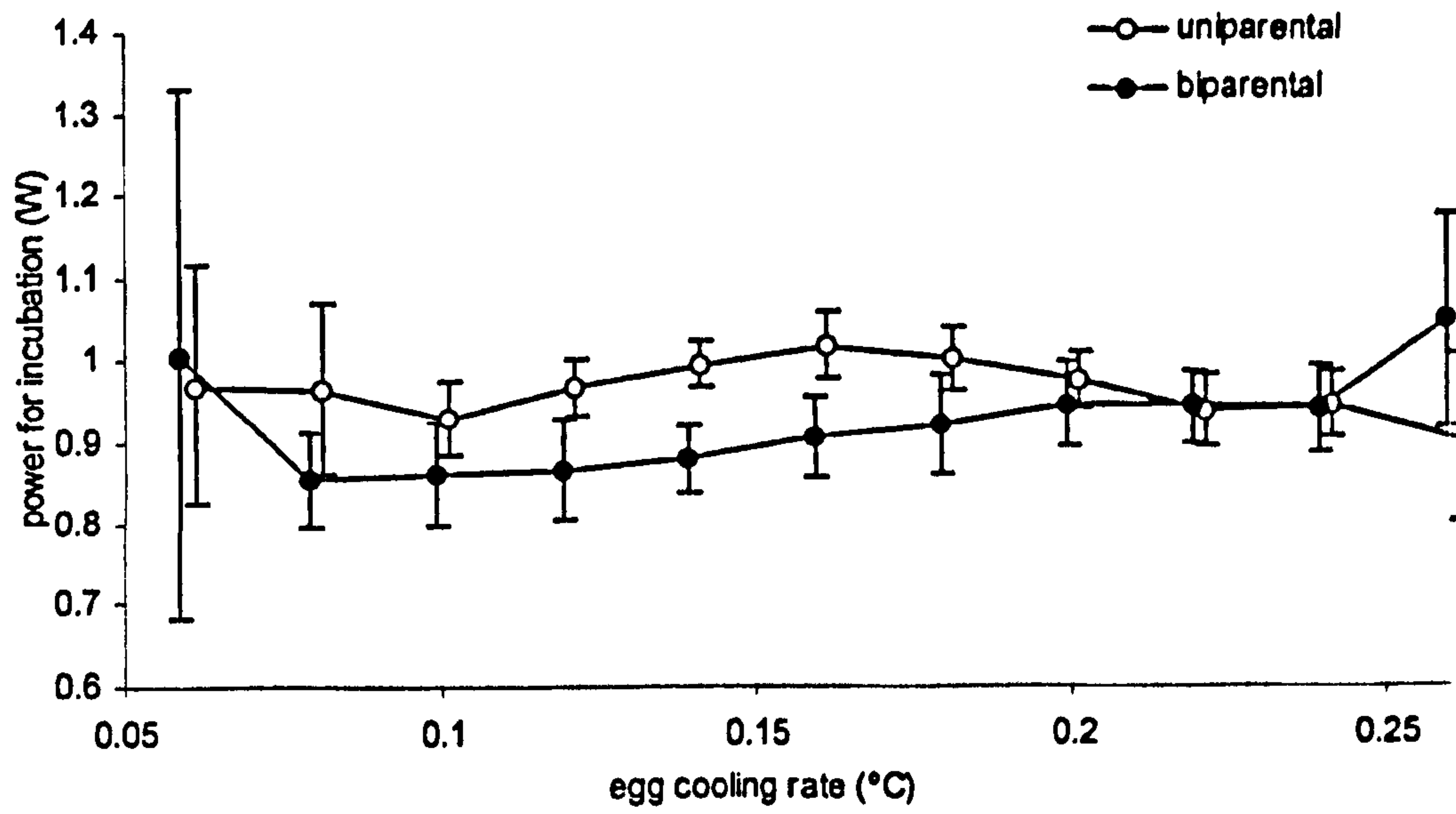


Figure 30. The estimated power expended on incubation with egg cooling rate and parental care (means  $\pm$  95% c.l., points offset slightly to allow error bars to be seen, between six and eight biparental nests and 31 and 38 uniparental nests used to calculate each mean).

## Stage of Incubation

### *Nest attendance*

Nest attendance declined through the incubation period (Chapter 3). As there was insufficient statistical power to include interaction terms in the model in Chapter 3, this analysis did not test whether the pattern of attendance with stage of incubation differed between parental care systems. Simplified tests that did not include any of the terms relating to energetic costs or food intake, showed that while the attendance of uniparental nests declined through the incubation period, the attendance at biparental nests increased significantly (GLM of nest attendance: uniparental, days since first egg date  $F_{1,491}=23.155$ ,  $P<0.001$ , partial  $R^2=0.045$ ,  $\beta=-0.00276$ , nest identity  $F_{37,491}=6.808$ ,  $P<0.001$ , partial  $R^2=0.339$ , model  $R^2_{\text{adj}}=0.316$ ; biparental, days since first egg date  $F_{1,144}=16.973$ ,  $P<0.001$ , partial  $R^2=0.105$ ,  $\beta=0.00183$ , nest identity  $F_{7,144}=7.520$ ,  $P<0.001$ , partial  $R^2=0.268$ , model  $R^2_{\text{adj}}=0.274$ , the samples were confined to first egg days whose mean was calculated from at least four nests but the test remained poorly balanced with  $51\% \pm 6\%$  and  $83\% \pm 8\%$  of uniparental and biparental nests, respectively, contributing a datum to each day from first egg date, Fig. 31). Energetic constraints affect nest attendance (Chapter 3) but as the index of costs did not vary with stage of incubation (Chapter 3) this probably did not introduce any bias into the two last tests.

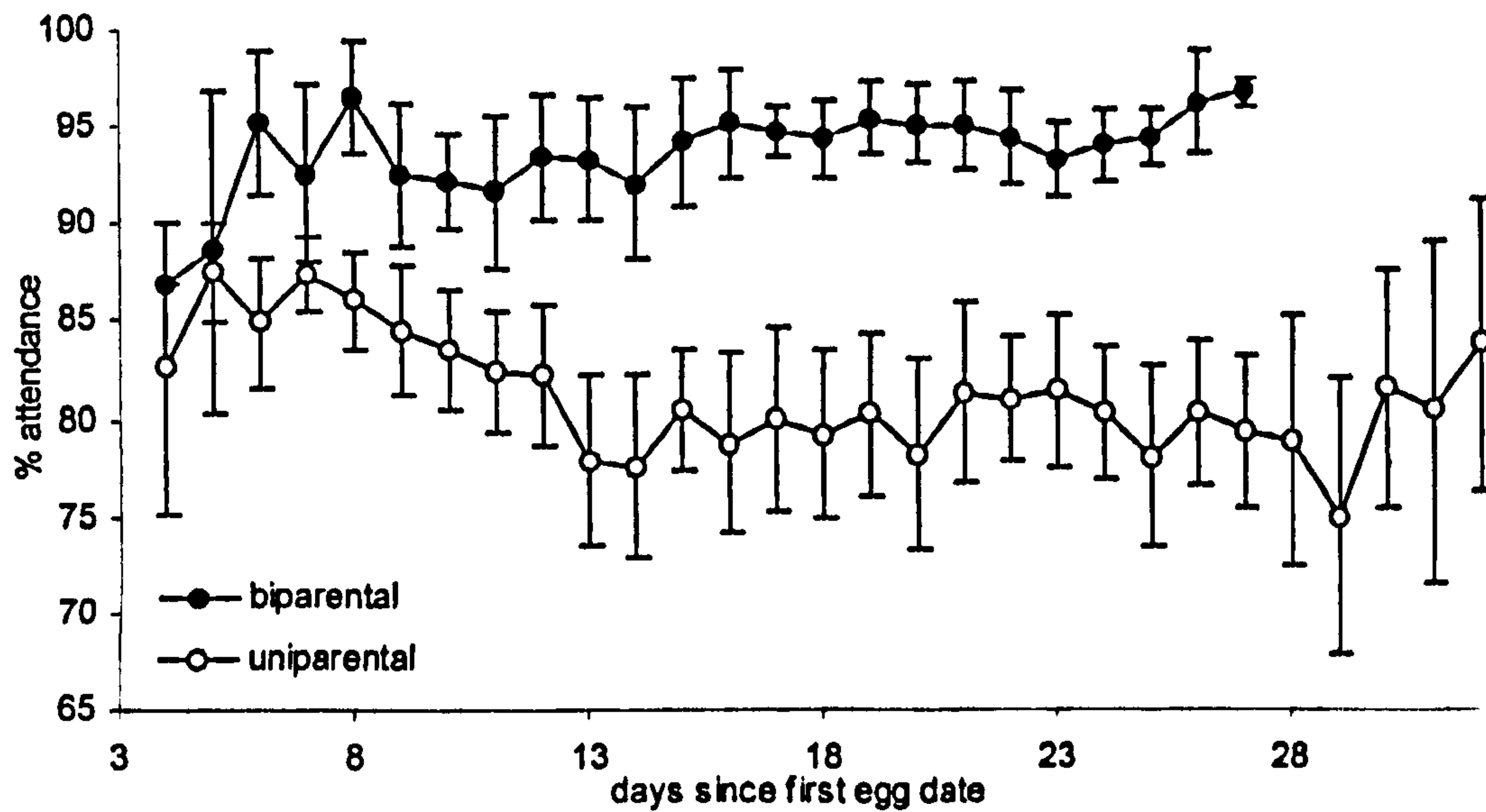


Figure 31. Nest attendance with stage of incubation and first egg date (mean  $\pm$  95% c.i. calculated for between three and 25 uniparental nests and between four and eight biparental nests).

*Trip duration*

Trip length did not vary with days since first egg date at either uniparental or biparental nests (GLM of trip length with days since first egg date: uniparental  $F_{1,26}=0.552$ ,  $P=0.464$ ; biparental  $F_{1,20}=2.229$ ,  $P=0.151$ , parametric tests used as the median of nest median trip length approximated the normal distribution, Figs. 32 & 33).

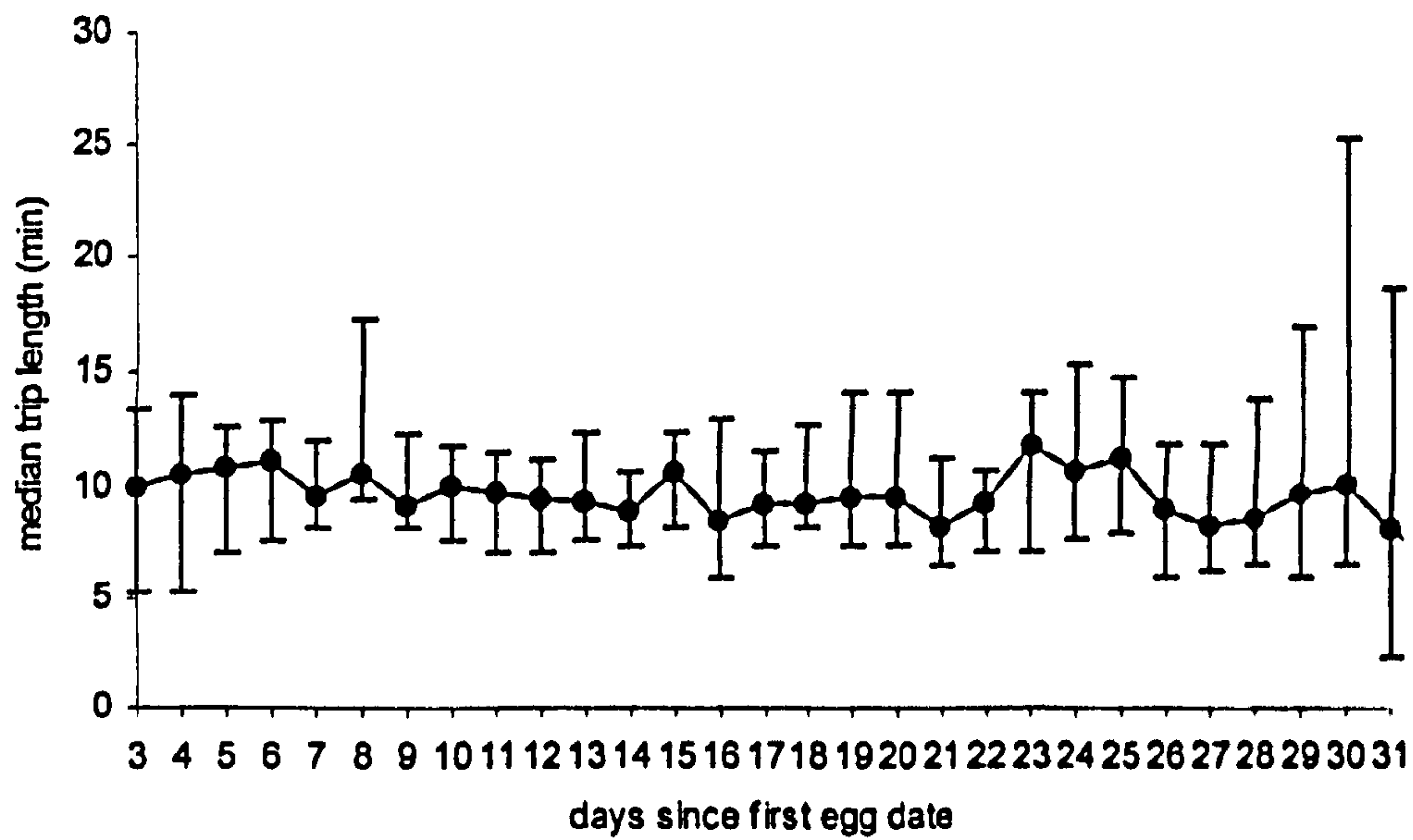


Figure 32. Trip length (median  $\pm$  95% c.i.) for uniparental nests with days since first egg date (medians were calculated from the median values from between 6 and 27 nests for each day since first egg date).

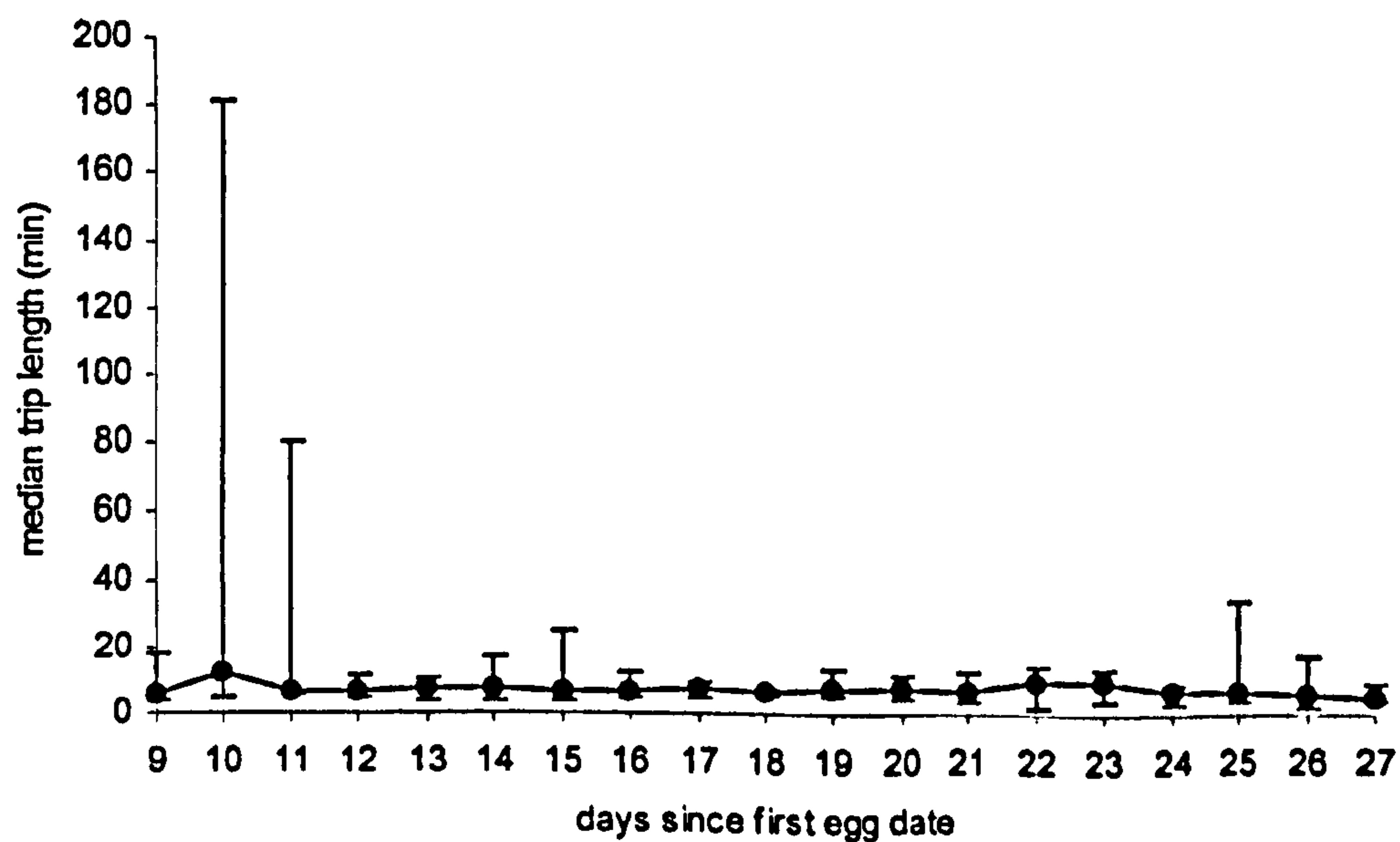


Figure 33. Trip length (median  $\pm$  95% c.i.) for biparental nests with days since first egg date (medians were calculated from the median values from between six and eight nests, which allowed calculation of confidence limits and confined the sample to days nine to 27 from first egg date).

### Incubation bout duration

Incubation bout duration decreased significantly with days since first egg date at uniparental nests (GLM of trip length with days since first egg date:  $F_{1,26}=34.059$ ,  $P<0.001$ ,  $R^2_{adj}=0.550$ ; biparental  $F_{1,20}=0.141$ ,  $P=0.771$ , using only days when the median was calculated from at least four nests, parametric tests used as the median of nest median incubation bout duration approximated the normal distribution, Fig. 34).

Incubation bout duration did not vary significantly with days since first egg date at biparental nests (GLM of trip length with days since first egg date:  $F_{1,20}=0.141$ ,  $P=0.771$ , using only days when the median was calculated from at least four nests, parametric tests used as the median of nest median incubation bout duration approximated the normal distribution, Fig. 35).

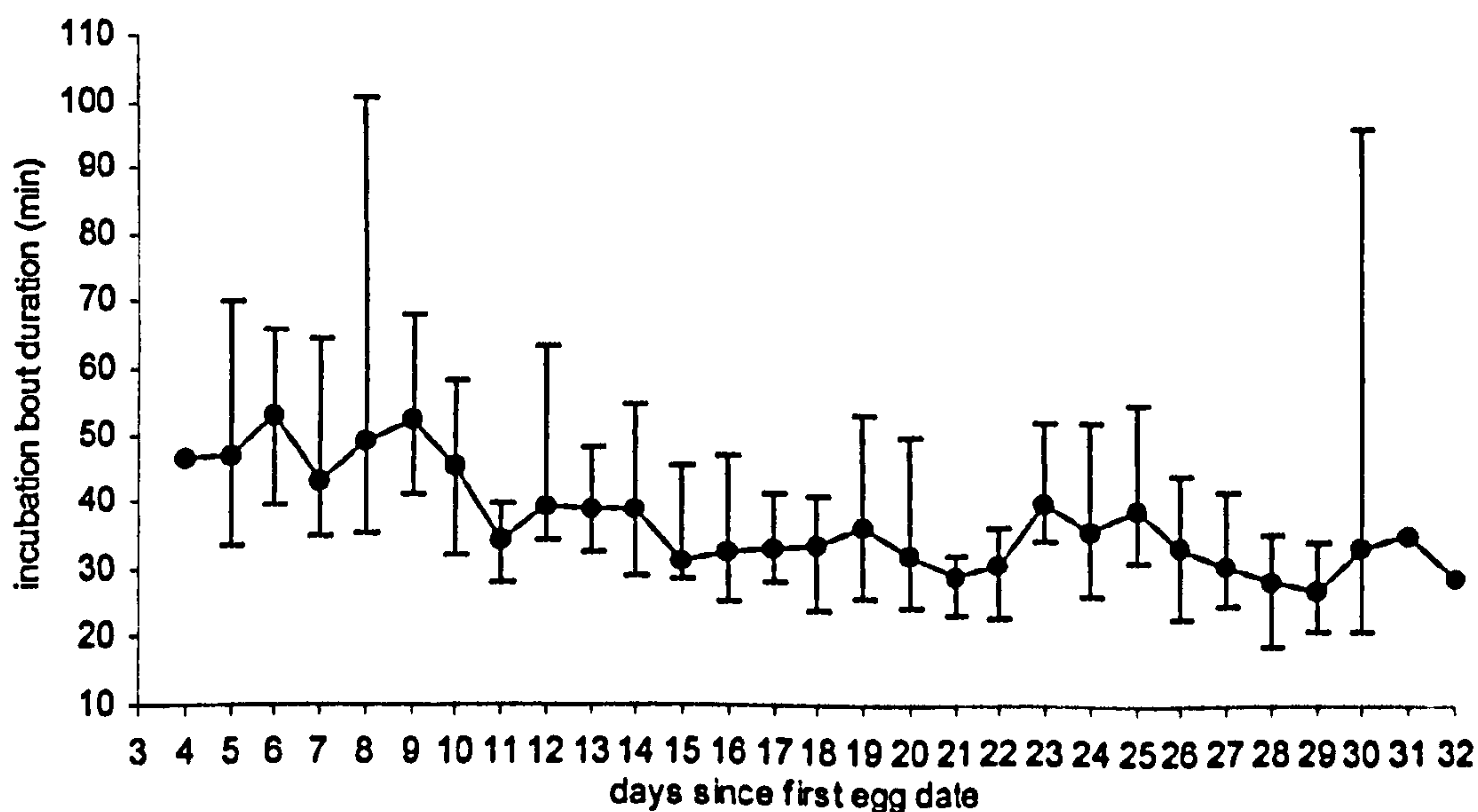


Fig 34. Incubation bout duration with stage of incubation for uniparental nests (median  $\pm$  95% c.i. of nest medians for between eight and 25 nests).

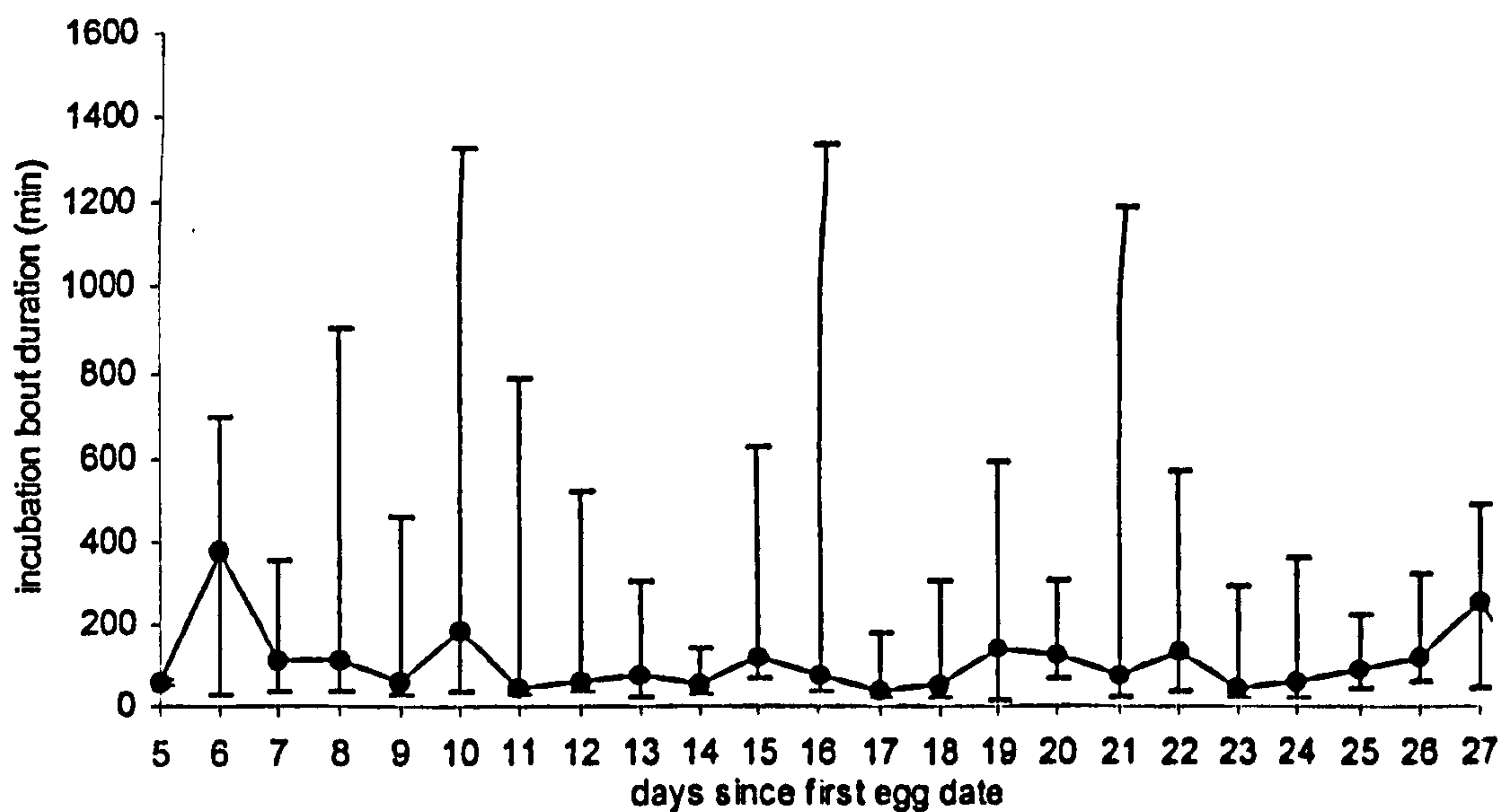


Fig 35. Incubation bout duration with stage of incubation for biparental nests (median  $\pm$  range of daily medians for between four and eight nests).

#### *Trip frequency*

The number of trips per hour increased significantly with days since first egg date at uniparental nests (GLM: days since first egg date  $F_{1,491}=30.207$ ,  $P<0.001$ , partial  $R^2=0.058$ ,  $\beta=0.0107$ , nest identity  $F_{37,491}=6.679$ ,  $P<0.001$ , partial  $R^2=0.335$ , model  $R^2_{adj}=0.325$ , the sample was confined to days from first egg date whose values were estimated from at least four nests: the test remained poorly balanced with  $51\% \pm 6\%$  of nests contributing a datum to each day since first egg date, Fig. 36).

The number of trips per hour decreased significantly with days since first egg date at biparental nests (GLM: days since first egg date  $F_{1,144}=18.788$ ,  $P<0.001$ , partial  $R^2=0.115$ ,  $\beta=-0.0103$ , nest identity  $F_{7,144}=16.899$ ,  $P<0.001$ , partial  $R^2=0.451$ , model  $R^2_{adj}=0.453$ , the sample was confined to days from first egg date whose values were estimated from at least four nests: the test remained poorly balanced with  $83\% \pm 6\%$  of nests contributing a datum to each day since first egg date, Fig. 37).



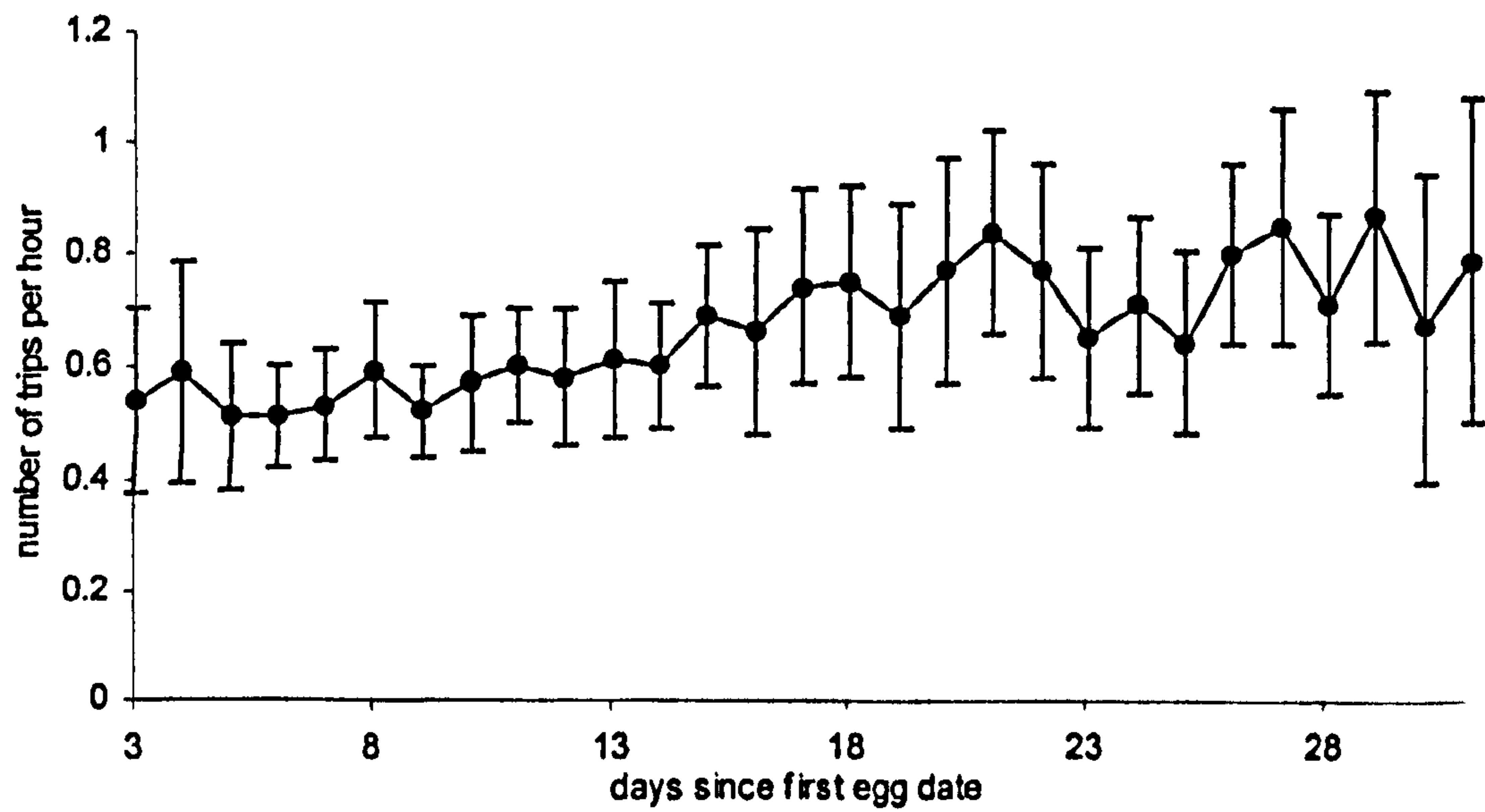


Figure 36. Trip rate with stage of incubation for uniparental nests (mean  $\pm$  95% c.i. for between six and 27 nests).

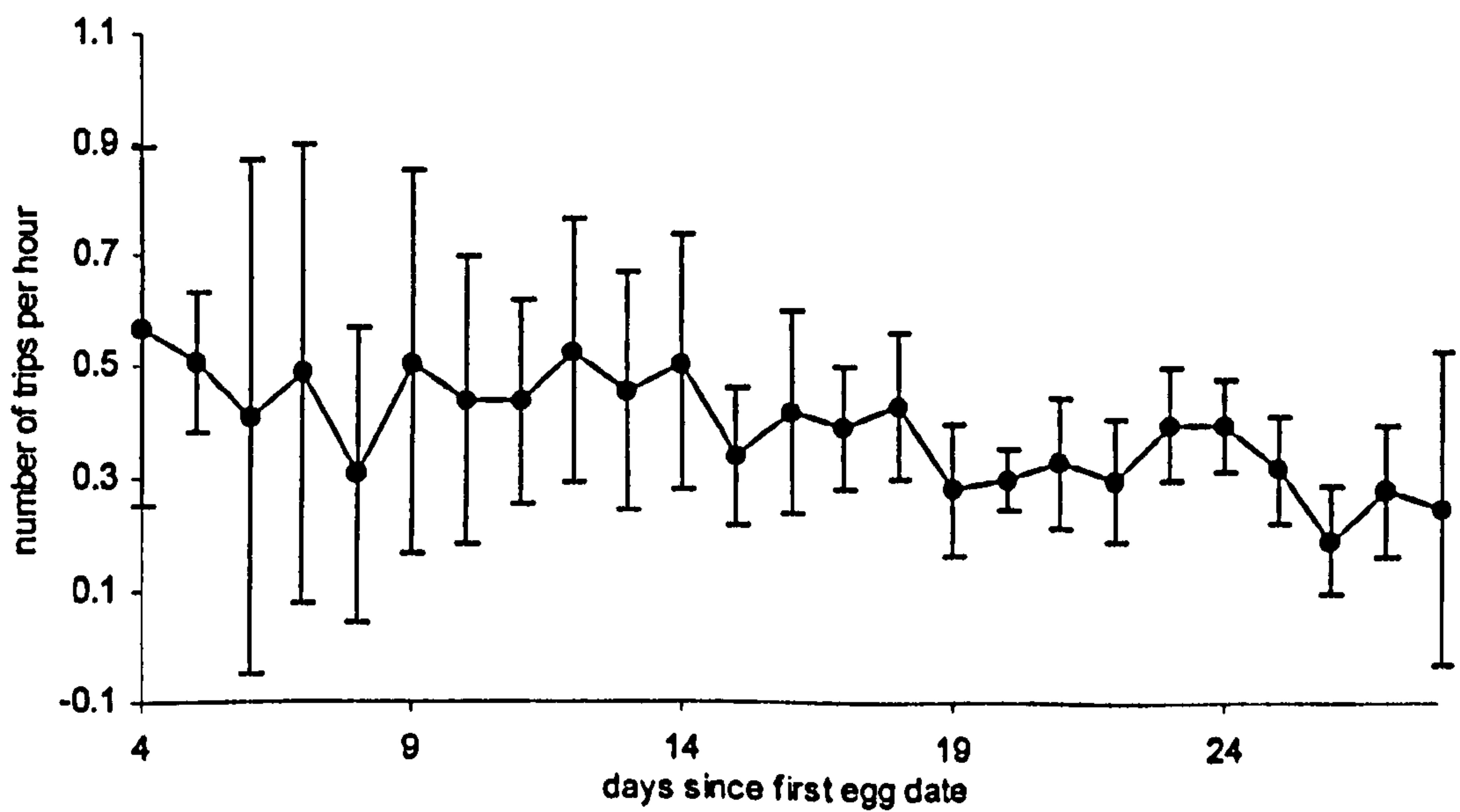


Figure 37. Trip rate with stage of incubation for biparental nests (mean  $\pm$  95% c.i. for between four and eight nests).

*Proportion of time eggs below 20°C*

The estimated proportion of time that eggs of uniparental nests spent below 20°C increased significantly through the incubation period (Chapter 3, Fig. 38).

The proportion of time that eggs spent below 20°C decreased significantly with days since first egg date at biparental nests (GLM: days since first egg date  $F_{1,144}=7.855$ ,  $P=0.006$ , partial  $R^2=0.052$ ,  $\beta=-0.107$ , nest identity  $F_{7,144}=2.811$ ,  $P=0.009$ , partial  $R^2=0.120$ , model  $R^2_{adj}=0.111$ , the sample was confined to days from first egg date whose values were estimated from at least four nests: the test remained poorly balanced with  $83\% \pm 6\%$  of nests contributing a datum to each day since first egg date, Fig. 39).

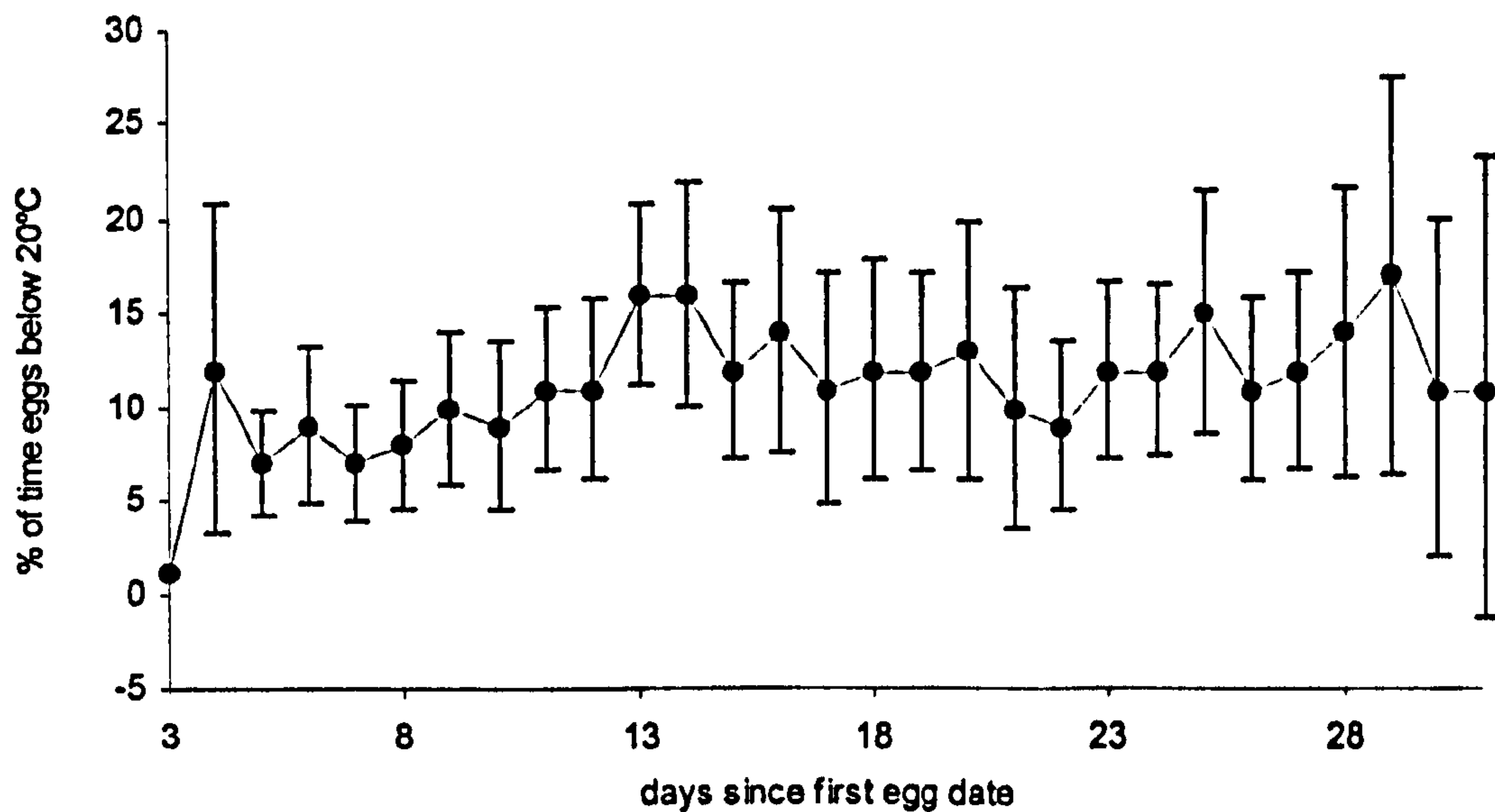


Figure 38. The estimated percentage of time that eggs of uniparental nests spend below 20°C (mean  $\pm$  95% c.i. for between five and 25 nests).

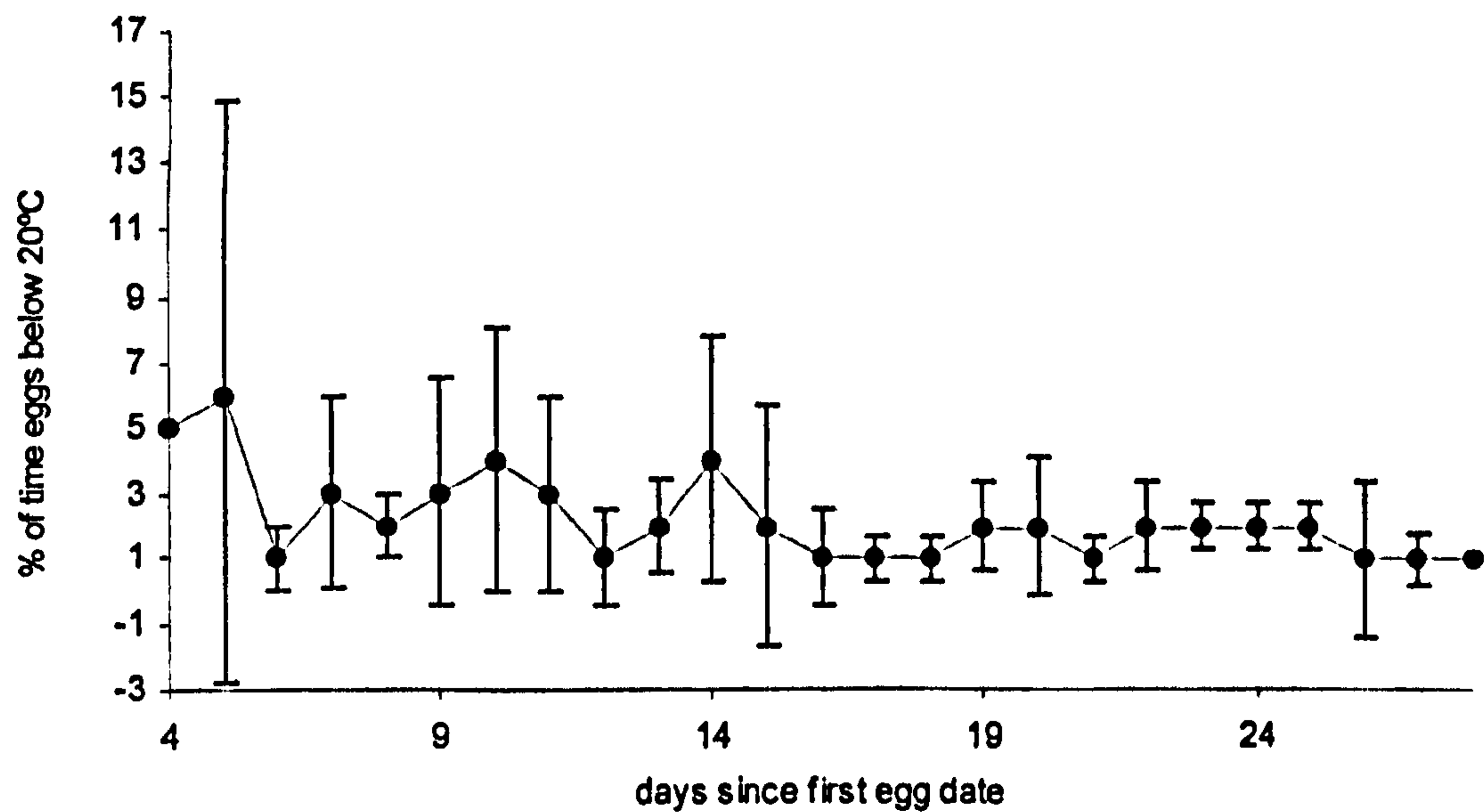


Figure 39 The estimated percentage of time that eggs of biparental nests spend below 20°C (mean  $\pm$  95% c.i. for between four and eight nests).

*Incidence of egg neglect*

The frequency of days on which neglect occurred did not vary significantly with days since first egg date at uniparental nests (GLM of the proportion of nests in which neglect occurred:  $F_{1,26}=0.559$ ,  $P=0.461$ , using only values calculated from at least four nests, Fig. 40). No test was done on biparental nests, where egg neglect was very rare (Fig. 41).

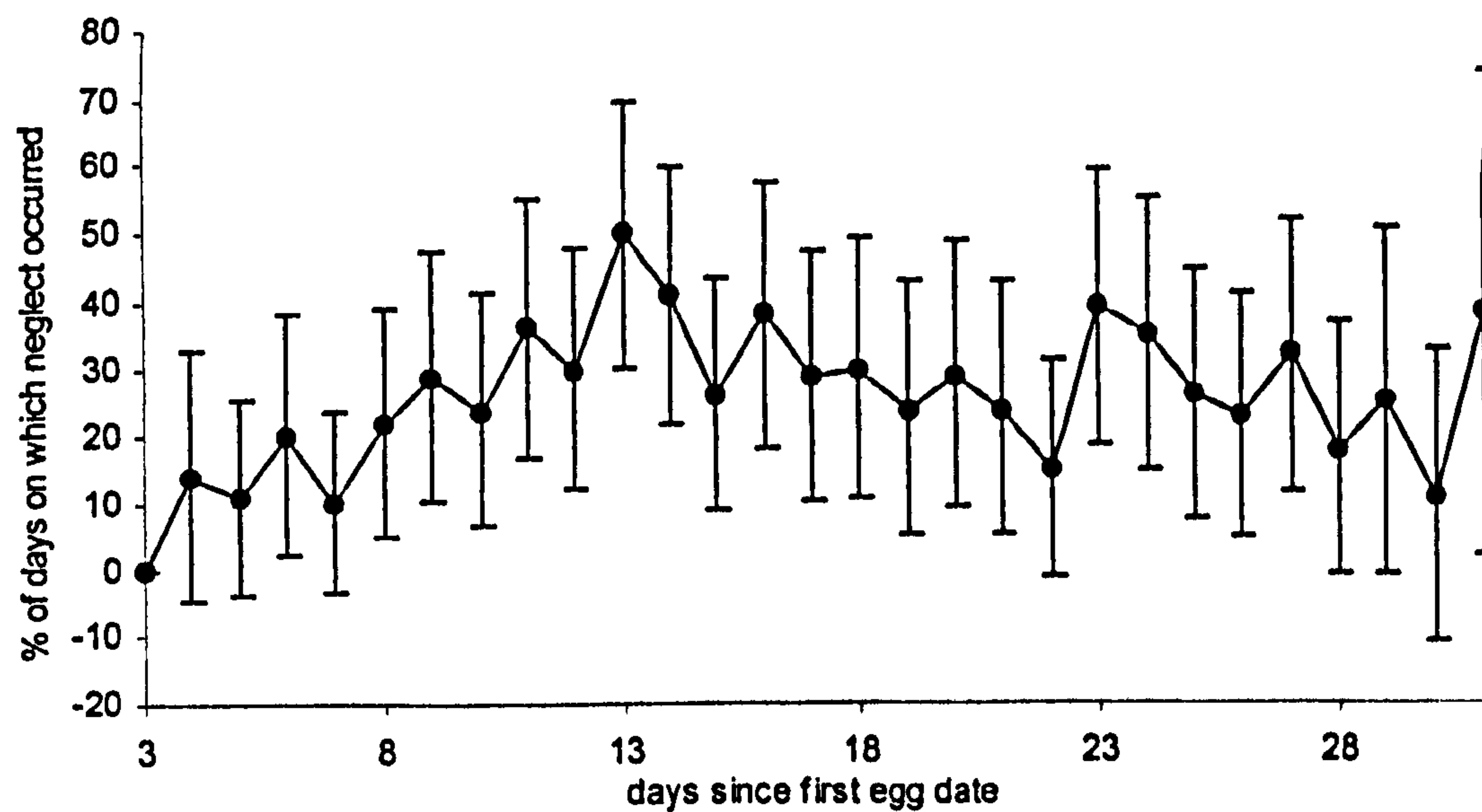


Figure 40. The percentage of days on which uniparental nests were neglected (mean  $\pm$  95% c.i. for between five and 25 nests).

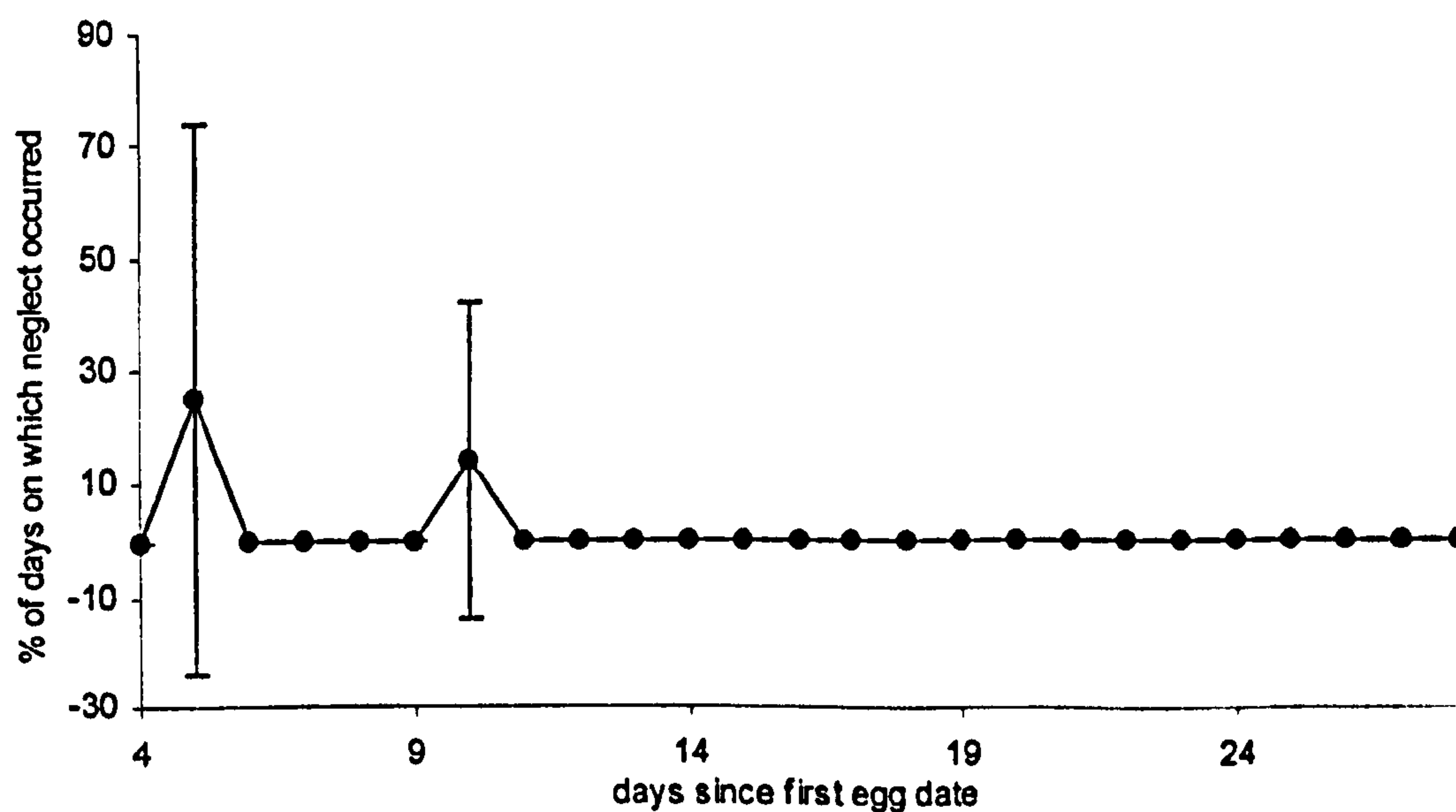


Figure 41. The percentage of days on which biparental nests were neglected (mean  $\pm$  95% c.i. for between four and eight nests).

#### *Power for incubation*

The power expended on incubation did not vary significantly with days since first egg date at uniparental nests (GLM: days since first egg date  $F_{1,491}=1.429$ ,  $P=0.233$ , partial  $R^2=0.003$ ,  $\beta=0.00107$ , nest identity  $F_{37,491}=7.360$ ,  $P<0.001$ , partial  $R^2=0.357$ , model  $R^2_{adj}=0.318$ , the

sample was confined to days from first egg date whose values were estimated from at least four nests: the test remained poorly balanced with  $51\% \pm 6\%$  of nests contributing a datum to each day since first egg date, Fig. 42).

The power expended on incubation decreased significantly with days since first egg date at biparental nests (GLM: days since first egg date  $F_{1,144}=48.810$ ,  $P<0.001$ , partial  $R^2=0.253$ ,  $\beta=-0.00666$ , nest identity  $F_{7,144}=16.279$ ,  $P<0.001$ , partial  $R^2=0.442$ , model  $R^2_{adj}=0.517$ , the sample was confined to days from first egg date whose values were estimated from at least four nests: the test remained poorly balanced with  $83\% \pm 6\%$  of nests contributing a datum to each day since first egg date, Fig. 43).

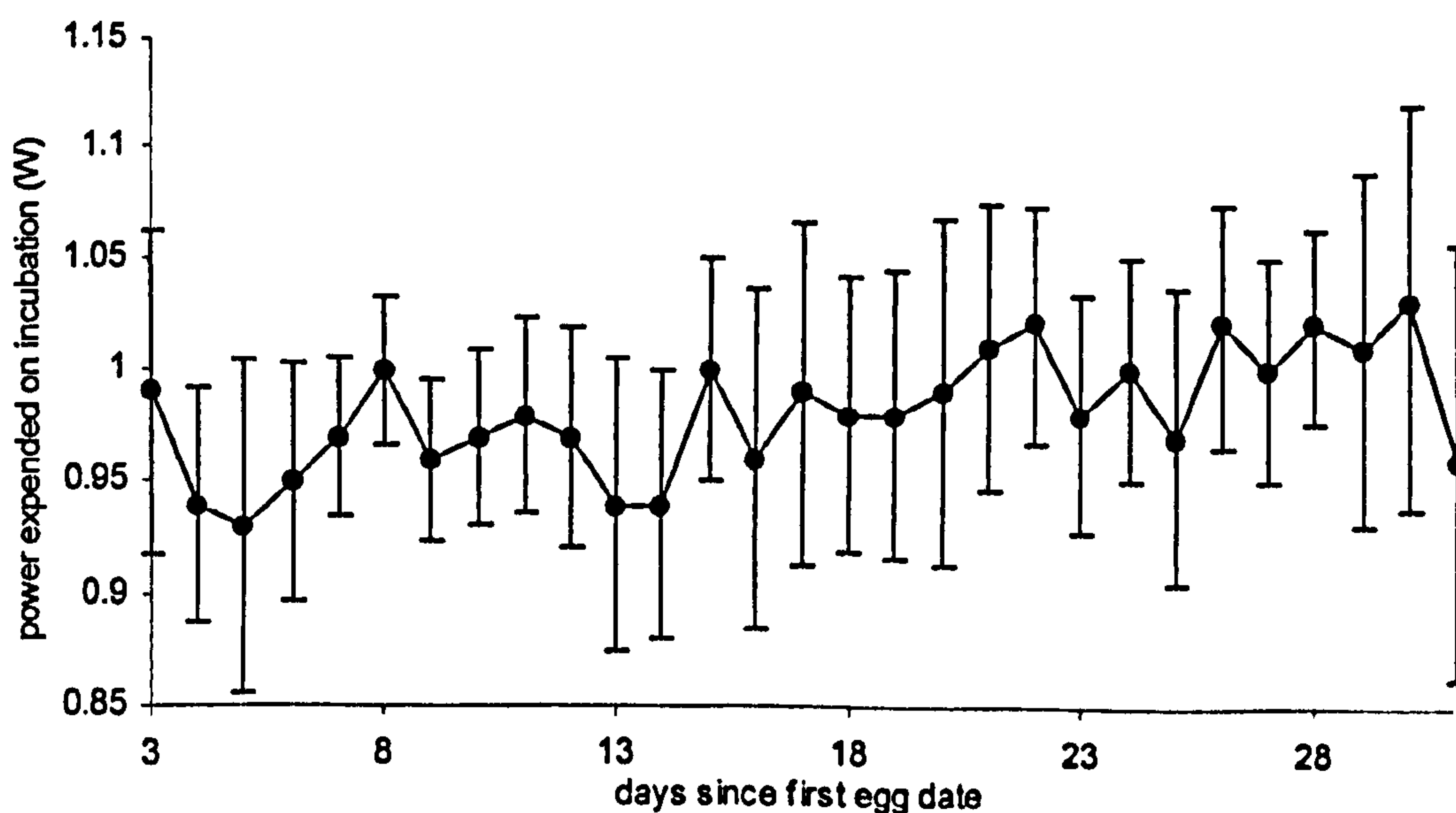


Figure 42. The power expended on incubation at uniparental nests (mean  $\pm$  95% c.i. for between five and 25 nests).

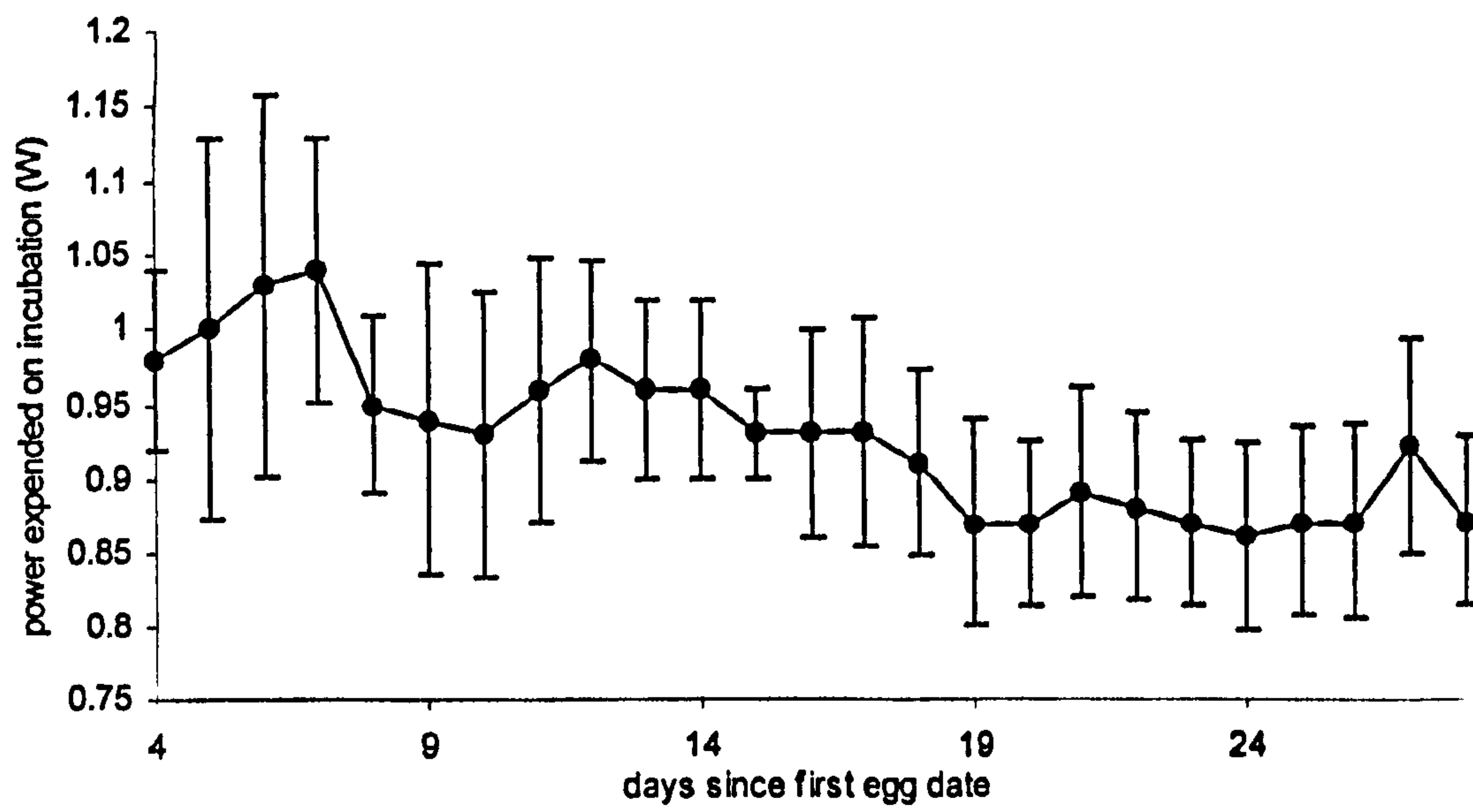


Figure 43. The power expended on incubation at biparental nests (mean  $\pm$  95% c.i. for between four and eight nests).

### Variation between nests

There was significant variation in nest attendance between nests (Chapter 3), which could be brought about by varying either trip duration or frequency (variation in incubation bout duration will be fully described by variation in these two). Variation between the attendance at uniparental nests was significantly influenced by trip duration but not by trip frequency (GLM of mean daily percentage attendance: median of daily median trip duration  $F_{1,32}=5.550$ ,  $P=0.025$ , partial  $R^2=0.148$ ,  $\beta=-0.904$ , mean daily trip frequency  $F_{1,32}=2.247$ ,  $P=0.144$ , partial  $R^2=0.148$ ,  $\beta=7.87$ , model  $R^2_{\text{adj}}=0.324$ , used only nests with at least five days attendance recorded). Attendance at biparental nests decreased significantly with both trip rate and trip duration (GLM of mean daily percentage attendance: median of daily median trip duration  $F_{1,5}=7.888$ ,  $P=0.038$ , partial  $R^2=0.612$ ,  $\beta=-0.652$ , mean daily trip frequency  $F_{1,5}=20.916$ ,  $P=0.006$ , partial  $R^2=0.807$ ,  $\beta=-11.3$ , model  $R^2_{\text{adj}}=0.756$ , used only nests with at least five days attendance recorded).

Uniparental nest attendance did not vary with the degree of wind exposure of a nest (calculated from the model in Chapter 3) or the volume of the nest lining or nest scrape, when controlling for the significant effects of the level of body stores of the parent (mass residualised for wing length and the stage of incubation, Holt et al. 2002, Chapter 3) and for the significant effects of the availability of *Tipula montana* and past and current energetic costs (GLM on the attendance nest coefficients from the GLM in Table 2 Chapter 3: residual mass  $F_{1,12}=11.374$ ,  $P=0.006$ , partial  $R^2=0.487$ ,  $\beta=0.3104$ ; wind exposure  $F_{1,12}=0.015$ ,  $P=0.903$ , partial  $R^2=0.001$ ,  $\beta=-1.55$ ; lining volume  $F_{1,12}=0.209$ ,  $P=0.656$ , partial  $R^2=0.017$ ,  $\beta=-0.00551$ ; scrape volume  $F_{1,12}=0.223$ ,  $P=0.646$ , partial  $R^2=0.018$ ,  $\beta=0.0000$ , model  $R^2_{\text{adj}}=0.368$ , scrape volume  $\text{mm}^3$  was estimated from scrape diameter and depth as a cylinder). Only 55% of the sample had known residual masses so, to increase statistical power, the test was repeated without controlling for mass. When a term for mass was not included in the analysis, uniparental percentage nest attendance did not vary with the degree of wind exposure of a nest or the volume of the nest lining but increased with the volume of the nest scrape (GLM on the attendance nest coefficients from the GLM in Table 2 Chapter 3: wind exposure  $F_{1,28}=0.171$ ,  $P=0.682$ , partial  $R^2=0.006$ ,  $\beta=-3.68$ ; lining volume  $F_{1,28}=0.277$ ,

$P=0.603$ , partial  $R^2=0.010$ ,  $\beta=-0.000566$ ; scrape volume  $F_{1,28}=6.876$ ,  $P=0.014$ , partial  $R^2=0.197$ ,  $\beta=0.000001149$ , model  $R^2_{\text{adj}}=0.132$ ). The effect of scrape volume when mass was removed was not due to association between the two as residual mass and scrape volume were not significantly correlated (Pearson correlation:  $r=-0.283$ ,  $N=17$ ,  $P=0.271$ ). Lining volume was significantly, positively correlated with scrape volume (Pearson correlation:  $r=0.468$ ,  $N=32$ ,  $P=0.007$ ), so scrape volume probably accounted for any effects of lining volume, with the additional effect of allowing more of the parents body to sit inside the cup, potentially decreasing the energetic cost of thermoregulation (Chapter 6).



## Did dotterel have to schedule incubation to prevent embryonic overheating?

During the two years of this study it appeared that none of the embryos in unattended dotterel eggs were exposed to dangerously high temperatures (Fig. 44).

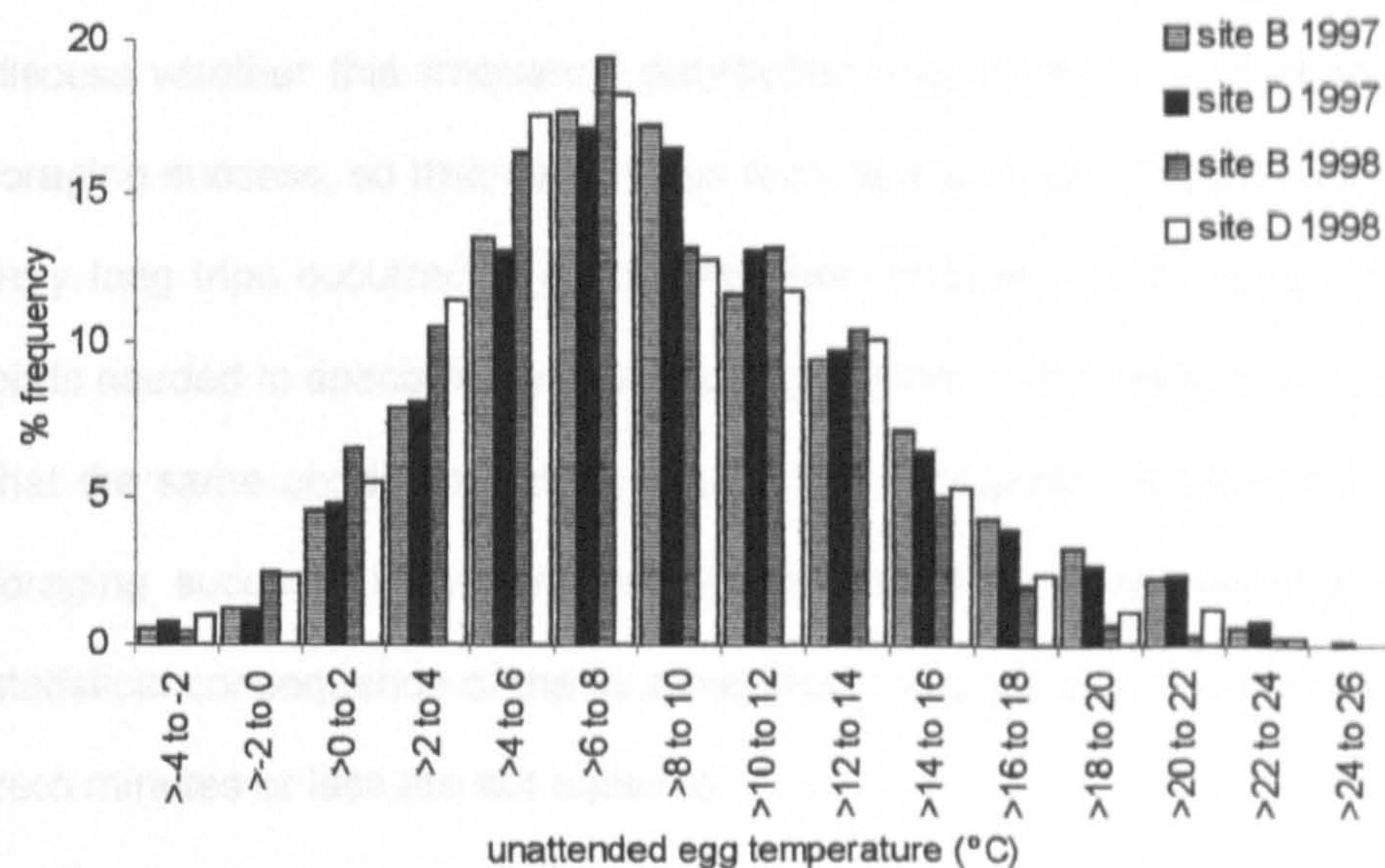


Figure 44. The estimated temperatures of permanently unattended eggs while dotterel nested. (Our estimate of unattended egg temperature, based on plaster filled dotterel eggs and unviable dotterel eggs, did not take into account any heat produced by embryonic metabolism. In live eggs the warming effect of embryonic metabolism may be cancelled out by the increased cooling rate caused by embryonic circulation, Turner 1991, and the relatively high cooling rate of unattended eggs will rapidly result in low metabolic rates in the exothermic embryos, Mathiu et al. 1994).

## Discussion

### *Trip duration*

The distribution of trip lengths was strongly skewed, with a long right hand tail, as in a number of other species (review in Cartar & Montgomerie 1985). Cartar & Montgomerie (1985) discuss whether this frequency distribution might reflect the probability distribution of their foraging success, so that longer trips represent periods of lower foraging success. In dotterel very long trips occurred in conditions when energetic costs were higher (Chapter 4) so that birds needed to spend more time feeding to meet these costs, but we cannot discount the fact that the same conditions might reduce prey availability (MacLean & Pitelka 1971), lowering foraging success. However, the asymmetry of the distribution may at least partly be a statistical consequence of the fact that trips far longer than the mean are possible, but trips of zero minutes or less are not possible.

The estimate of trip length depended greatly on the summary statistic used. The modal trip duration for both uniparental and biparental nests was between four and six minutes while the mean of daily medians was longer for uniparental nests at  $9.4 \pm 0.9$  min than biparental nests at  $7.2 \pm 1.2$  min. The mean trip duration from uniparental nests was longer in this study than those in a Norwegian study (uniparental nests: Norway  $8.7 \pm 0.7$  min, this study  $19.1 \pm 4$  min; biparental nests: Norway  $9.4 \pm 0.5$  min, this study  $9.8 \pm 1.6$  min, Kålås 1986). Because of the strong skew in the distribution of trip durations, means provide a poor estimate of central tendency and the higher uniparental mean trip length in this study may have reflected a greater number of very long trips, rather than a difference in typical trip duration. Trip rate did not differ significantly between the two studies (uniparental nests: Norway  $0.96 \pm 0.17$  hr<sup>-1</sup>, this study  $0.68 \pm 0.07$  hr<sup>-1</sup>; biparental nests: Norway  $0.65 \pm 0.22$  hr<sup>-1</sup>, this study  $0.39 \pm 0.11$  hr<sup>-1</sup>, Kålås 1986).

### *Parental care system*

Attendance differences between parental care systems in dotterel appeared to vary between this study and other studies: biparental nests 94% ( $\pm 1\%$ , this study, eight nests), 96%

(Pulliainen & Saari 1997, one nest), 91% ( $\pm$  2%, Kálás 1986, 6 days of recorded nest attendance); uniparental nests 81% ( $\pm$  2%, this study, 38 nests), 73% ( $\pm$  7%, Pulliainen & Saari 1994, 7 nests), 89% ( $\pm$  1%, Kálás 1986, 37 days of recorded nest attendance) and 88% (Wilkie 1981, one nest).

In a Norwegian study of dotterel, (Kálás 1986) there was no significant difference in nest attendance between parental care systems, in contrast to this study in Scotland. In this study there was overlap between the highest nest attendance at uniparental nests and the lowest nest attendance at biparental nests. The degree of energetic constraint that birds experience during the incubation period may vary in space and time (Siikamaki 1995). Nest attendance at uniparental nests was limited by energetic constraint (Chapter 3), so that the Norwegian dotterel may have been experiencing less energetic constraint. However, both Scottish and Norwegian dotterel lost a similar amount of mass through the incubation period, only about one third of Finnish dotterel's loss, suggesting that dotterel in the Scottish and Norwegian studies may have experienced similar levels of energetic constraint. Dotterel seemed to use the energetically less costly tight-sitting response to predators when more energetically constrained (Chapter 7) and there is further weak evidence for the ranking of the degree of energetic constraint experienced in the three studies in their patterns of nest defence. Dotterel in this Scottish study flushed at significantly shorter distances than in Byrkjedal's (1987) study on the Norwegian site (S. Holt et al. unpublished data) and Pulliainen & Saari (1995) believed that dotterel in their Finnish study flushed at much shorter distances than those in the Norwegian study. Of course, there may be reasons other than energetic constraint for the higher uniparental nest attendance in Norway and also the differences in mass loss and nest defence. A different predator assemblage, higher predation risk or higher egg cooling rate could compel uniparental Norwegian dotterel to spend more time on the nest.

Biparental dotterel achieved their higher nest attendance through shorter and less frequent trips and their high nest attendance meant that their eggs spent less time below a temperature suitable for development. Although higher nest attendance can make incubation less energetically expensive, the shorter trips from biparental nests and their lack of

synchronisation with conditions when eggs cooled more slowly (Chapter 3) meant that no less energy was expended on incubation at biparental nests than at uniparental nests, although the costs borne by each individual were lower as shared.

#### *Variation with time of day*

White-rumped sandpipers *Calidris fuscicollis* and other shorebirds made their longest trips in the late morning and afternoon, and their shortest trips at night (review in Cartar & Montgomerie 1985) and white-rumped sandpipers made trips more frequently around midday (Cartar & Montgomerie 1985). As a consequence of this diurnal variation in trip length and frequency, nest attendance was lowest around midday. The uniparental common snipe *Gallinago gallinago* only made trips from the nest during daylight, although wintering snipe and male snipe during the breeding season forage mainly during darkness (Green et al. 1990). Daylight nest attendance in snowy plovers *Charadrius alexandrinus* was lowest in late afternoon and peaked in the late evening: the late afternoon dip may correspond to ambient temperatures when the unattended eggs will remain at a temperature suitable for development without overheating (Purdue 1976). In the Alaskan arctic, attendance showed a weak decline in the middle of the day in the biparental dunlin *Calidris alpina* and Baird's sandpiper *C. bairdii* and a much more marked decline during the lightest half of the day in the uniparental pectoral sandpiper *C. melanotos* (Norton 1972). Norton (1972) suggests that pectoral sandpipers concentrated their foraging in the lightest parts of the day to maximise their ability to see prey, but this explanation does not appear very general as common snipe and uniparental dotterel, which can forage at night, had reduced attendance during daylight (Green et al. 1990).

The daylight pattern of nest attendance in uniparental white-rumped sandpipers, great snipe *Gallinago media*, pectoral sandpipers and dotterel (Kondratiev 1982; Cartar & Montgomerie 1985; Løfaldli 1985; Kálás 1986; Pulliainen & Saari 1994; Pulliainen & Saari 1997) is quite similar (Chapter 3) and bird species from other groups may follow a similar pattern (Williams & Dwinell 1990; Williams 1993). Both dotterel and white-rumped sandpipers appeared to be responding to the typical diurnal variation in weather conditions, rather than light or dark *per*

se in their patterns of nest attendance. White-rumped sandpipers appeared to track mean cooling rates by having a circadian pattern of nest attendance that was modified by current weather conditions (Cartar & Montgomerie 1985).

Uniparental dotterel's variation in attendance with time of day was a consequence of variation in both trip frequency and trip duration. The proportion of time that eggs spent below a temperature suitable for development followed the pattern of attendance. Most periods of egg neglect were initiated between mid-morning and early afternoon. If a dotterel must leave the nest unattended for a long time, trips made at this time may pose least chilling risk to the embryos. Alternatively, this timing might provide the best feeding conditions or there may be variation in the risk of egg predation, while neglected, with time of day. The estimated power for incubation was highest during the pre-dawn and midnight period of increased feeding activity in both uniparental and biparental nests. The higher rate of feeding trips during the middle of the day at uniparental nests was not reflected in an increased cost of incubation. The lower egg cooling rates at this time of day must have compensated for the increased number of times the eggs were rewarmed and the longer trips. The lack of any increase in costs was probably not due to decreased costs of steady state incubation during the day as the costs of steady state incubation did not vary between daylight and darkness at uniparental nests.

We found variation in the pattern of daily nest attendance in biparental dotterel, although other biparental shorebirds may not vary their schedule in this way (reviewed in Cartar & Montgomerie 1985), sometimes because the nest is rarely unattended other than during brief changeovers (Cresswell et al. in press).

If the activity of nest predators varies with the light conditions and the parent's incubation scheduling affects the probability of clutch predation, the pattern of nest attendance might be expected to vary with the light level (Cartar & Montgomerie 1985). Uniparental nest attendance was higher during darkness while biparental nest attendance was lower during darkness (at uniparental nests this was because trips were shorter but no less frequent during

darkness). Uniparental and biparental dotterel both had pre-dawn and midnight peaks in trips off the nest and the principal difference in their pattern of incubation scheduling with time of day was that biparental parents did not increase the amount of time that the nest was unattended in the middle of the day.

Although some of the periods of inattendant at biparental nests were probably changeovers (although changeovers may be virtually instantaneous in some shorebird species, Cresswell et al. in press), biparental parents also made feeding trips like those of uniparental parents during their incubation shift, at which time the nest was unattended (pers. obs.).

Biparental dotterel appeared to be less energetically constrained than uniparental dotterel and did not match their feeding trips to the times of day when their egg rewarming costs would be lowest (Holt et al. 2002, Chapter 3). The less energetically constrained biparental dotterel spent a greater proportion of their time off the nest during darkness than uniparental dotterel. Uniparental dotterel were probably compelled to feed more during the daytime when unattended eggs cooled more slowly because they were more energetically constrained. The biparental daily pattern of attendance probably represents a more optimal pattern that was allowed when energetic constraint was reduced or absent. However, it would be too simplistic to suggest that foraging during darkness was preferable, as the night time trips were concentrated into a period around midnight and a period just before dawn at both uniparental and biparental nests. In a Norwegian study, dotterel appeared to also have a peak in time off the nest around midnight but lacked the pre-dawn peak (Kålås 1986). If darkness *per se* was the reason for lower overall attendance then trips should have been evenly distributed throughout the night or distributed in relation to the level of darkness. The pre-dawn and midnight peaks in time off the nest probably gave an advantage not associated with the energetic costs of incubation, such as a reduced risk of clutch predation or coincided with peaks in prey availability.

### *Variation with egg cooling rate or weather conditions*

Dotterel varied their incubation scheduling according to the energetic costs they had to bear, which were determined by weather conditions (Chapter 3). The analyses of how incubation scheduling varied with the rate of egg cooling gave less clear results, probably because egg cooling rate varies both in a predictable daily pattern and unpredictably, dependent on current weather conditions, and because egg cooling rate is correlated with factors that determine the degree of energetic constraint dotterel were experiencing. Uniparental dotterel's response to the predictable daily variation probably involved scheduling trips in the typically most advantageous part of the day. Dotterel's response to variation in egg cooling rate due to weather systems probably depended on the degree of energetic constraint they were under.

Wind appeared to be the most important weather variable in incubation scheduling in white-rumped sandpipers (Cartar & Montgomerie 1985), which compressed their feeding trips into the warmest part of the day on windier days. In this study, the relative importance of different weather variables was incorporated into the models of the costs of thermoregulation and incubation and egg cooling rate (Chapter 3). Wind speed and ambient temperatures varied greatly while dotterel were incubating and were important factors in the models of both the cost of thermoregulation and incubation so that they must have been important influences on the degree of energetic constraint dotterel experienced. The effect of precipitation was taken into account in the rate of egg cooling, but not into the costs of thermoregulation or steady state incubation (wetter ground may have higher heat conductivity, Rosenberg 1974) and this may account for some of the unexplained variation in the analyses in Chapter 3.

### *Variation through the incubation period*

Webb (1987) suggests that parents may increase their investment later in the incubation period in order to maintain egg temperature closer to the optimum. Attendance in the biparental herring gull *Larus argentatus* increased as incubation progressed. This occurred through a combination of longer incubation shifts and shorter periods while the nest was unattended (Drent 1970), although all these trends were reversed shortly before hatch.

Similarly, attendance by snowy plovers *Charadrius alexandrinus* increased through the incubation period (Purdue 1976). However, there was no evidence that attendance changed through the incubation period on completed clutches of dunlin *Calidris alpina*, semipalmated sandpiper *C. pusilla*, pectoral sandpiper *C. melanotos* or Baird's sandpiper *C. bairdii* breeding in the arctic or in northern lapwings *Vanellus vanellus* or bar-tailed godwits *Limosa lapponica* (Norton 1972; Hegyi & Sasvári 1998).

As in a Norwegian study (Kálás 1986), we found a decline in attendance amongst uniparental dotterel through the incubation period. A Finnish study (Pulliainen & Saari 1994) found no decline in attendance, possibly because of lower power from a smaller sample of nests. Attendance declined with stage of incubation at uniparental nests (Chapter 3), but further analysis in this chapter showed that attendance increased through the incubation period at biparental nests. This supports the idea that declining attendance at uniparental nests was due to increasing energetic constraint as body reserves were depleted: biparental dotterel had higher body reserves and were anyway probably less constrained due to greater foraging time (Holt et al. 2002).

As in the Norwegian study (Kálás 1986), uniparental dotterel's decline in attendance was proximately due to an increase in trip frequency, rather than trip duration and biparental dotterel's increase in attendance was due to a decrease in trip frequency through the incubation period. Trip duration did not vary with stage of incubation at uniparental or biparental nests. The declining attendance of uniparental nests and the increasing attendance of biparental nests resulted in increasing and decreasing amounts of time spent below a temperature suitable for development, respectively. Parents at biparental nests achieved their increase in attendance and the consequent improvement in their embryos' thermal environment through the incubation period, while decreasing their energetic expenditure on incubation: at the trips lengths from biparental nests, the cost of incubation was predicted to decrease with increasing attendance (Chapter 3). Single parents did not change their energetic expenditure on incubation through the incubation period, but the greater time spent off the nest will have improved their energy budget, unless prey availability also changed. It is,



perhaps, surprising that the incidence of egg neglect at uniparental nests did not increase through the incubation period as dotterel appeared to be increasingly energetically constrained and dotterel embryos appeared to be very tolerant of chilling throughout their development (Chapter 4).

For a few days following clutch completion, Charadriiformes may neglect their nest during the night (Drent 1970 & references therein), possibly partly because incubation may be less effective (i.e. result in a lower rate of embryonic development) early in the incubation period if the brood patches are not yet fully developed (Drent 1970). Nocturnal neglect may allow parents to retreat to locations where their risk of predation is lower but may increase their eggs' risk of predation (Drent 1970). Nocturnal desertion may only be a successful strategy early in incubation because the sensitivity of embryos to chilling can increase through the incubation period (Batt & Cornwell 1972), although this pattern may not apply to all species and may even be reversed in some (MacMullan & Eberhardt 1953; reviewed in Webb 1987; Deeming & Ferguson 1991). There was no evidence for a higher incidence of nocturnal neglect early in the incubation period in dotterel: nocturnal egg neglect was less common than daylight egg neglect, possibly because the low night time temperatures in an arctic-alpine environment might result in damaging embryo chilling, even in apparently tolerant species such as the dotterel.

#### *Variation between nests*

There was significant variation in nest attendance between uniparental nests (Chapter 3), some of which may have been due to different levels of body stores (although body stores and attendance may have been linked by a third factor such nest microclimate, foraging ability or habitat quality that affected the degree of energetic constraint dotterel experienced, rather than have a direct causal relationship between them). The level of body stores may also be related to nest attendance in other shorebird species (Cartar & Montgomerie 1985).

Our egg cooling rates were estimated using an artificial nest that simulated a nest in open *Racomitrium lanuginosum* heath. However, microclimate or microhabitat variables that may

affect rates of heat loss, such as wind speed, insolation, air temperature, ground temperature, the substrate and the degree of water saturation of the substrate, may vary between nest sites. Wind is a very important influence on shorebirds' energetic cost of thermoregulation (Wiersma & Piersma 1994) and also on the rate of egg cooling (Chapter 3) and the wind speed experienced at a nest varied with microhabitat features (Chapter 6). Although wind speeds at dotterel's level were high, there was no evidence that the wind exposure of a nest site affected incubation scheduling. Nest sites that gave protection from wind gave poorer views of approaching predators (Chapter 6) and birds may have only chosen more exposed nest sites with anti-predation benefits if they were better able to bear higher energetic costs (Hohman 1986).

There was evidence that larger scrapes were associated with higher nest attendance levels, possibly because of energetic savings by allowing a larger insulating nest lining and also more of the parent's body to fit in the scrape. In contrast, nest attendance was lower at better insulated Village Weaver *Ploceus cucullatus* nests (White & Kinney 1974). Village weavers belong to the set of bird species that, unlike dotterel, decrease nest attendance as ambient temperatures increase (White & Kinney 1974) and the lower rate of egg cooling that was probably associated with better insulated nests probably acted in the same way.

#### *How did dotterel vary their nest attendance?*

In white-rumped sandpipers, weather accounted for 32% of the variation in attendance but only 12% of the variation in trip length was accounted for by weather so that Cartar & Montgomerie (1985) concluded that attendance was principally varied through trip frequency. They suggest that this method of varying nest attendance is typical of small species, while larger species instead increase the duration of trips away from the nest, an energetically cheaper strategy with lower egg rewarming costs. White & Kinney (1974) suggested that uniparental intermittent incubators generally vary attendance by changing the duration of incubation bouts, although they also reviewed exceptions where attendance also varied with changing trip duration. In dotterel, whether it was trip frequency or trip duration that principally affected nest attendance depended upon which samples were being compared. Variation in

nest attendance through the day was achieved by varying both trip duration and trip frequency, with trip frequency accounting for more variation. However, in contrast to Cartar & Montgomerie's (1985) suggested pattern for smaller species, variation between uniparental dotterel nests was due to differences in trip duration alone. The daily pattern of nest attendance of uniparental shorebirds nesting in the Asian arctic arose through variation in trip duration alone (Kondratiev 1982).

Unless individuals change their trip lengths there may be a positive feedback effect in having to spend more time off the nest, as individuals that make more foraging trips incur greater egg rewarming costs, necessitating more time spent foraging off the nest (Chapter 3). This positive feedback effect could potentially exacerbate the effect of energetic constraint on nest attendance, although it appears that when individuals need to spend more time foraging they reschedule incubation to increase trip length and cap their energetic cost of incubation (Chapter 3). More energetically constrained individuals might, then, be expected to increase trip length as well as decrease nest attendance. Between uniparental nests, lower nest attendance arose through longer rather than more frequent trips. Kálás & Løfaldli (1987) found that two dotterel with low masses reduced their nest attendance by making few but longer trips per day and, in an analysis that pooled variation within and between individuals, heavier dotterel varied their nest attendance through trip frequency. In summary, Kálás & Løfaldli's (1987) birds with small body reserves and the uniparental dotterel in this study used the energetically cheaper strategy of varying attendance through trip duration. In contrast, Kálás & Løfaldli's (1987) dotterel with greater body reserves varied attendance through trip frequency, which though potentially more energetically costly, may provide a better thermal environment for the embryos.

*Did dotterel have to schedule incubation to prevent embryonic overheating?*

We did not formulate any hypotheses of how dotterel should vary their incubation scheduling to prevent their embryos overheating: using our model of unattended egg temperature with weather variables (Chapter 3), we estimate that permanently unattended eggs would spend no time at damagingly high temperatures (Fig. 44). The two years of this study were

particularly cool and wet and dotterel may have to act to prevent embryonic overheating in other parts of their range or in other years in this area: in hot, sunny weather in the Highlands of Scotland dotterel have been observed to shade eggs and pant, suggesting conditions when unattended eggs might overheat (pers. obs.; Nethersole-Thompson 1973).

In summary, dotterel's incubation scheduling is typified by a large number of relatively short trips (Kålås 1986). The incubation scheduling of uniparental and biparental nests differed in a number of ways, which probably reflected the different degree of energetic constraint experienced. Incubation scheduling parameters in this study appeared to differ from those in other studies of dotterel and this may reflect differing degrees of energetic constraint or, alternatively, may be an artefact of comparing small sample sizes between studies. Both uniparental and biparental nests showed variation in nest attendance through the day and although the pattern of attendance during darkness was similar, only uniparental dotterel had a peak in the amount of time the nest was unattended in the middle of the day. Dotterel may spend more time off the nest by increasing trip duration, which increases the time the eggs spent at a temperature unsuitable for development, or by increasing trip frequency, which pushes up the energetic cost of incubation. Within the day, dotterel varied the time they spent off the nest through trip frequency and, less importantly, trip duration. However, variation in attendance between nests was due to differing trip durations. Variation in attendance between nests was also related to the level of body stores and the size of the nest scrape: larger scrapes, which may reduce energetic costs, were associated with higher nest attendance. Nest attendance declined through the incubation period at uniparental nests, but increased at biparental nests because of changing trip frequency.

## References

- Baerends, G.P., Drent, R.H., Glas, P. & Groenewold, H. 1970. An ethological analysis of incubation behaviour in the Herring Gull. Behaviour Supplement , 17, 135-234.
- Batt, B.D. & Cornwell, G.W. 1972. The effects of cold on Mallard embryos. Journal of Wildlife Management , 36, 745-751.

- Byrkjedal, I. 1987. Antipredator behaviour and breeding success in Greater Golden Plover and Eurasian Dotterel. The Condor , 89, 40-47.
- Calder, W.A. 1973. An estimate of the heat balance of a nesting hummingbird in a chilling climate. Comparative Biochemistry and Physiology , 46, 291-300.
- Campbell, R.C. 1989. Statistics for biologists . Third Edition edn. Cambridge: Cambridge University Press.
- Cartar, R.V. & Montgomerie, R.D. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. Behaviour , 95, 261-289.
- Cartar, R.V. & Montgomerie, R.D. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. The Condor , 89, 252-260.
- Cramp, S. & Simmons, K.E.L. 1983. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic; Volume 3: Waders to Gulls. Oxford: Oxford University Press.
- Cresswell, W., Holt, S., Reid, J.B., Whitfield, D.P. & Mellanby, R. In Press. The effects of steady state incubation costs on incubation scheduling in semipalmated sandpipers Behavioural Ecology
- Deeming, D.C. & Ferguson, M.W.J. 1991. Physiological effects of incubation temperature on embryonic development in reptiles and birds. In: Egg incubation: its effects on embryonic development in birds and reptiles (Ed. by D.C. Deeming & M.W.J. Ferguson), pp. 147-171. Cambridge: Cambridge University Press.
- Downs, C.T. & Ward, D. 1997. Does shading behavior of incubating shorebirds in hot environments cool the eggs or the adults? Auk , 114, 717-724.
- Drent, R.H. 1970. Functional aspects of incubation in the Herring Gull. Behaviour Supplement , 17, 1-132.
- Erikstad, K.E., Myrberget, S. & Blom, R. 1982. Territorial crows as predators on Willow Ptarmigan nests. Journal of Wildlife Management , 46, 109-114.
- Grant Carey, C., Hoyt, D.F., and Kendeigh, S.C., editors. Avian incubation: egg temperature, nest humidity and behavioural thermoregulation in a hot environment. Washington, D.C.: The American Ornithologists Union. (1982). p.1 30. Ornithological Monographs.

- Green,R.E., Hirons,G.J.M. & Cresswell,B.H. 1990. Foraging habitats of female Common Snipe *Gallinago gallinago* during the incubation period. Journal of Applied Ecology , 27, 325-335.
- Harvey,J.M. 1971. Factors affecting Blue Goose nesting success. Canadian Journal of Zoology , 49, 223-234.
- Hegyi,Z. & Sasvári,L. 1998. Parental condition and breeding effort in waders. Journal of Animal Ecology , 67, 41-53.
- Hohman,W.L. 1986. Incubation rhythms of Ring-necked Ducks. The Condor , 88, 290-296.
- Holt,S., Whitfield,D.P., Duncan,K., Rae,S. & Smith,R.D. 2002. Mass loss in incubating Eurasian dotterel: adaptation or constraint? Journal of Avian Biology , 33, 219-224
- Horsfield,D. & Thompson,D.B. 1996. The uplands: guidance on terminology regarding altitudinal zonation and related terms. Information and Advisory Note 26. Battleby, UK: SNH
- Inglis,I.R. 1977. The breeding behaviour of the Pink-footed Goose: behavioural correlates of nesting success. Animal Behaviour , 25, 747-764.
- Kálás,J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). Ardea , 74, 185-190.
- Kálás,J.A. & Løfaldli,L. 1987. Clutch size in the Dotterel *Charadrius morinellus*: an adaptation to parental incubation behaviour? Ornis Scandinavica , 18, 316-319.
- Kondratiev,A.J. 1982. Biology of waders in the tundras of the north-east of Asia. Academy of Sciences of the USSR: Nauka, Moscow
- Løfaldli,L. 1985. Incubation rhythms in the Great Snipe *Gallinago media*. Holarctic Ecology , 8, 107-112.
- MacLean,S.F.Jr. & Pitelka,F.A. 1971. Seasonal patterns of abundance in tundra arthropods near Barrow, Alaska. Arctic , 24, 19-40.
- MacMullan,R.A. & Eberhardt,L.L. 1953. Tolerance of incubating pheasant eggs to exposure. Journal of Wildlife Management , 17, 322-330.
- Martin,T.E. & Ghalambor,C.K. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation? American Naturalist , 153, 131-139.

- Miskelly,C.M. 1989. Flexible incubation system and prolonged incubation in New Zealand Snipe. Wilson Bulletin , 101, 127-132.
- Nethersole-Thompson,D. 1973. The Dotterel. Glasgow: Collins.
- Norton,D.W. 1972. Incubation schedules of four species of Calidrine sandpipers at Barrow, Alaska. The Condor , 74, 164-176.
- Norusis,M.J. 1990. SPSS/PC+ Advanced Statistics 4.0. Gorinchem: SPSS Ltd.
- Parmelee,D.F. 1970. Breeding behaviour of the sanderling in the Canadian high arctic. Living Bird , 9, 97-146.
- Pulliainen,E. & Saari,L. 1994. Incubation behaviour of the Dotterel *Charadrius morinellus*. Oecologia Montana , 3, 27-34.
- Pulliainen,E. & Saari,L. 1995. Inter- and intraspecific reactions of Incubating Dotterel *Charadrius morinellus* in Finland. Wader Study Group Bulletin , 78, 36-38.
- Pulliainen,E. & Saari,L. 1997. Attendance at the nest of polyandrous Dotterel *Charadrius morinellus* in Finland. Ardea , 85, 67-71.
- Purdue,J.R. 1976. Thermal environment of the nest and related parental behaviour in snowy plovers, *Charadrius alexandrinus*. The Condor , 78, 180-185.
- Rosenberg,N.J. 1974. Microclimate: the biological environment. New York: John Wiley & Sons.
- Siikamaki,P. 1995. Are large clutches costly to incubate? - the case of the Pied Flycatcher. Journal of Avian Biology , 26, 76-80.
- Webb,D.R. 1987. Thermal tolerance of avian embryos: A review. The Condor , 89, 874-898.
- White,F.N. & Kinney,J.L. 1974. Avian incubation. Science , 186, 107-115.
- Wiebe,K.L. & Martin,K. 1997. Effects of predation, body condition and temperature on incubation rhythms of White-tailed Ptarmigan. Wildlife Biology , 3, 219-227.
- Wiersma,P. & Piersma,T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. The Condor , 96, 257-279.
- Wilkie,A.O.M. 1981. Incubation Rhythm and behaviour of a Dotterel *Charadrius morinellus* nesting in Norway. Ornis Fennica , 58, 11-20.
- Williams,J.B. 1993. Energetics of incubation in free-living Orange-breasted Sunbirds in South Africa. The Condor , 95, 115-126.

Williams, J.B. & Dwinell, B. 1990. Incubation energetics of female Savannah Sparrows.

Physiological Zoology , 63, 353-372.

Zerba, E. & Morton, M.L. 1983. Dynamics of incubation in Mountain White-crowned Sparrows.

The Condor , 85, 1-11.



## APPENDIX: OTHER PRODUCTS OF THE STUDY

Timing of nest departure by broods of Eurasian dotterel

Potential reproductive rates in the Eurasian dotterel *Charadrius morinellus*

SHORT REPORT

## Timing of nest departure by broods of Dotterel *Charadrius morinellus*

SUE HOLT<sup>1</sup>\* and D. PHILIP WHITFIELD<sup>2</sup>

<sup>1</sup>University of Stirling, UK and <sup>2</sup>Scottish Natural Heritage, Edinburgh, UK

**Capsule** Most broods left during early to mid-morning, which may allow the small, largely exothermic chicks to emerge into a favourable thermal environment for feeding.

Most shorebirds (waders: Charadrii) nest on the ground. Mortality of their usually precocial and nidifugous chicks is highest in the first few days after hatch (D.P. Whitfield unpubl. data), probably because they are least capable of self-regulation of body temperature, most limited by the development of locomotory and feeding apparatus, and least able to evade predators (Visser & Ricklefs 1993a, Beintema & Visser 1989b). When shorebird chicks leave the nest may be important in maximizing their survival through this period, but the timing of departure and the factors that influence it have been rarely quantified. We describe the timing of nest departure by broods of the fully precocial and nidifugous Dotterel *Charadrius morinellus*, a shorebird that breeds in the harsh environment of the Palearctic arctic–alpine zone. Dotterels' clutches of typically three eggs are usually incubated by the male alone and all care of the chicks is carried out by the male.

Dotterel were studied on two sites in the Grampian mountains of the Scottish Highlands in 1997 and 1998 (the general methods are described elsewhere: Holt & Whitfield 1996, Galbraith *et al.* 1993). Nest occupancy was recorded using a small, flexible temperature probe fixed at the centre of the each nest and linked to a data logger. We assumed that broods departed from the nest when temperature readings indicated that the nest became empty, close to the date that the clutch was known or predicted to hatch. However, Ravens *Corvus corax* and, probably, mustelids depredated clutches during the study and we suspect that some apparent nest departures were actually predation events. To overcome this problem, we distinguished between

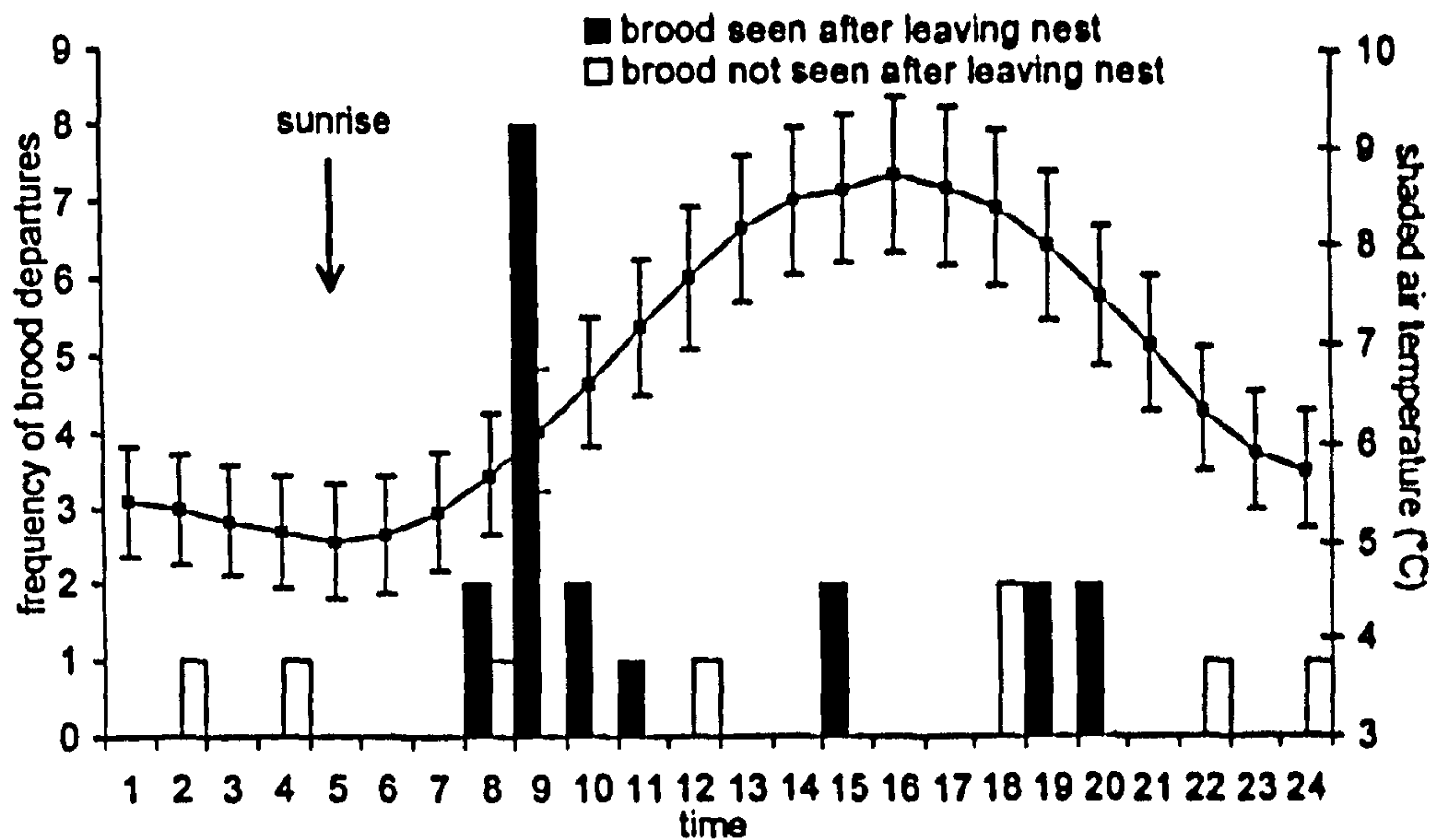
broods that were seen alive after nest departure and those that were not subsequently seen outside the nest and so may not have survived to depart (Fig. 1).

Most broods (63% of 19) that were definitely known to have left the nest did so between 07:00 and 10:00 hours. The vacation times of nests where broods may not have departed were more scattered through the day. This pattern of departure is unlikely to be a consequence of increased human disturbance at this time of day, as most hill walkers, who made up the majority of visitors to Dotterels' breeding grounds, arrived later (D.P. Whitfield unpubl. data). There was a very weak suggestion that trapping may have affected the departure times of some of the broods that definitely departed the nest; 43% of the 14 broods whose male parents were trapped at the nest did not depart during the peak period (07:00–10:00 hours) while only one (20%) of the five broods whose male parent was not trapped departed outside this time.

Only three of the nests were visited when the entire brood had hatched and in all cases the brood remained in the nest until the following morning (a mean of 17.3 hours between nest visit to brood departure). Nethersole-Thompson (1973) also describes how fully hatched Dotterel broods may delay leaving the nest until the following day and Pulliainen & Saari (1992) found that Dotterel broods left the nest between morning and early afternoon. In our study, none of the 19 broods that definitely left the nest did so in the dark or twilight. Darkness may increase the risk of the relatively slow-moving, newly hatched chicks being taken by nocturnal predators, although the anti-predation benefits of remaining in the nest are not obvious.

Waiting for daylight is not a wholly satisfactory explanation of delayed departure, as broods that

\*Correspondence author at: 34 Acre End Street, Eynsham, Oxfordshire, OX29 4PA, UK.  
Email sue@holtcress.freeserve.co.uk



**Figure 1.** Brood nest departure times (British Summer Time) and mean shaded air temperature ( $\pm$  95% CL, recorded 1.2 m above ground level for all dates in 1997 and 1998 that include 95% of the Julian dates on which Dotterel hatched). The mean time of sunrise for the same period (range 04:23 to 04:54 hours) is also indicated.

definitely left the nest only did so a median of 4.5 hours after sunrise (range 2.9–15.0 h, Fig. 1). Nethersole-Thompson & Nethersole-Thompson (1986) describe how the broods of a number of shorebird species remained in the nest until the following morning, especially in poor weather. Dotterels' arctic-alpine breeding habitat is cool, wet and windy: at the time when Dotterel broods left the nest, mean shaded air temperature was 6.9°C ( $n = 18$  broods), the mean wind speed estimated for 0.02 m above ground level was 4.3 m/s ( $n = 11$  broods) and it was either raining or thick mist for 21% of 19 broods. Dotterel chicks weigh around 11 g at hatching (Thomson 1994, Nethersole-Thompson & Nethersole-Thompson 1986, D.P. Whitfield unpubl. data) and are largely exothermic (Visser & Ricklefs 1993a, 1993b). In poor weather, the time spent being brooded may considerably reduce the time that chicks can forage and so compromise survival (Beintema & Visser 1989a, 1989b).

Shaded air temperature varied through the day (Fig. 1) so that the most common mid-morning departure time may trade-off a favourable temperature for departure against the total amount of available foraging time before the temperature starts to drop again late in the day. The higher levels of solar radiation during the day may also reduce foraging chicks' cooling rates. Additionally, the availability of invertebrate prey is likely to increase in the same warmer and sunnier conditions that increase their foraging time (MacLean & Pitelka 1971). Delayed nest departure may provide

the chicks with an improved thermal environment and foraging conditions on emergence but, in the meantime, the brood is confined to the nest area. However, the lined nest cup probably provides a good microclimate for brooding (Visser 1998) and, before final departure, individual chicks make short trips from the nest (Nethersole-Thompson 1973, pers. obs.), which may supplement their energy budgets or develop their foraging or locomotory abilities.

The role of the risk of nest-predation in nest departure timing is unclear, as we do not know whether predation risk is higher for chicks inside or outside the nest, and the diurnal pattern of variation in predation risk may depend on the local predator suite. The temporal pattern of Dotterel broods' nest departures is similar to that of a number of precocial wader and waterfowl species (review in Afton & Paulus 1992, Nethersole-Thompson & Nethersole-Thompson 1986).

Parents also apparently delayed departure from the nest to wait for inviable eggs to hatch: a single chick stayed in the nest with two inviable eggs for at least 72.4 hours after hatching before departure and, in the same hills in 1993, a chick remained in the nest for at least 211 hours while a further chick hatched and the remaining chick died during hatch (pers. obs). However, parents also abandoned hatching eggs and departed with the remaining chicks (one of 19 nests where broods definitely left; D.P. Whitfield unpubl. data). Parents may have assessed that the remaining

embryo had just died or, given the late or protracted hatch, would die. Alternatively, egg abandonment may represent a trade-off in which meeting the survival requirements of the hatched chicks gives the parent greater reproductive success than staying with the hatching eggs.

The conflict between caring for chicks and hatching eggs results from Dotterels' variably asynchronous hatch, caused by incubation starting before clutch completion (Pulliainen & Saari 1992, Kålås 1986, Nethersole-Thompson & Nethersole-Thompson 1986, Kålås & Byrkjedal 1984, Cramp & Simmons 1983). The degree of hatching asynchrony in Dotterels' relatively small clutches is perhaps surprising and difficult to explain, given the potential implications for reproductive success; hatching in other similarly sized temperate and arctic shorebird species seems more synchronous (Nethersole-Thompson & Nethersole-Thompson 1986, Cramp & Simmons 1983).

After nest departure, shorebird broods sometimes return to spend nights in the nest (Nethersole-Thompson & Nethersole-Thompson 1986). Return was not detected in the nest temperature traces of any of the 15 broods that had definitely left the nest and for which nest temperatures were monitored for at least one night after departure.

## REFERENCES

- Afton, A.D. & Paulus, S.L. 1992. Incubation and brood care. In Batt, B.D., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. (eds) *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis.
- Beintema, A.J. & Visser, G.H. 1989a. Growth parameters in chicks of charadriiform birds. *Ardea* **77**: 169–180.
- Beintema, A.J. & Visser, G.H. 1989b. The effect of weather on time budgets and development of chicks of meadow birds. *Ardea* **77**: 181–192.
- Cramp, S. & Simmons, K.E.L. 1983. *The Birds of the Western Palearctic*, Vol. 3: *Waders to Gulls*. Oxford University Press, Oxford.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D.P. & Thompson, D.B.A. 1993. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. *Ibis* **135**: 148–155.
- Holt, S. & Whitfield, D.P. 1996. Montane Ecology Project site report series: [site B]. Edinburgh: Scottish Natural Heritage.
- Kålås, J.A. 1986. Incubation schedules in different parental care systems in the Dotterel (*Charadrius morinellus*). *Ardea* **74**: 185–190.
- Kålås, J.A. & Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). *Auk* **101**: 838–847.
- MacLean, S.F. Jr. & Pitelka, F.A. 1971. Seasonal patterns of abundance in tundra arthropods near Barrow, Alaska. *Arctic* **24**: 19–40.
- Nethersole-Thompson, D. 1973. *The Dotterel*. Collins, Glasgow.
- Nethersole-Thompson, D. & Nethersole-Thompson, M. 1986. *Waders: Their Breeding, Haunts and Watchers*. T. & A.D. Poyser Waterhouses, Staffordshire, UK.
- Pulliainen, E. & Saari, L. 1992. Breeding biology of the Dotterel, *Charadrius morinellus*, in eastern Finnish Lapland. *Ornis Fenn* **69**: 101–107.
- Thomson, D.L. 1994. Growth and development in Dotterel chicks *Charadrius morinellus*. *Bird Study* **41**: 61–67.
- Visser, G.H. 1998. Development of temperature regulation. In Starck, J.M. & Ricklefs, R.E. (eds) *Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum*. Oxford Ornithology Series. Oxford University Press, Oxford.
- Visser, G.H. & Ricklefs, R.E. 1993a. Development of temperature regulation in shorebirds. *Physiol. Zool.* **66**: 771–792.
- Visser, G.H. & Ricklefs, R.E. 1993b. Temperature regulation in neonates of shorebirds. *Auk* **110**: 445–457.

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SHORT REPORT

## Potential reproductive rates in the Eurasian Dotterel *Charadrius morinellus*

SUE HOLT<sup>1</sup>\*, D. PHILIP WHITFIELD<sup>2</sup> and JAMES GORDON<sup>2</sup>

<sup>1</sup>University of Stirling, UK and <sup>2</sup>Scottish Natural Heritage, Edinburgh, UK

**Capsule** A female Eurasian Dotterel sequentially paired with five males within one season and bred with at least two.

The Eurasian Dotterel *Charadrius morinellus* is a sex-role-reversed shorebird: males carry out all care for the eggs and chicks in most breeding attempts and females are larger, have brighter plumage and are more active during courtship (Owens *et al.* 1994, Pulliainen & Saari 1992, Kålås 1988, Cramp & Simmons 1983). Emancipation from care of the eggs and young allows females to practice polyandry (Kålås & Byrkjedal 1984), with up to three sequential mates reported (Cramp & Simmons 1983). Here we report observations of a colour-ringed female Dotterel that sequentially paired with five different males in one breeding season. We use these observations to indicate large sexual differences in potential reproductive rates that are consistent with the direction of sexual selection in the Dotterel.

These observations were made over 52 visits between 3 May and 23 August 1998 to a low-alpine site in the Central Highlands of Scotland. The female was given a unique colour-ring combination as a yearling in 1997. Dotterel were classified as paired if they nest-scraped together (the action of hollowing out a nest cup, also used during courtship; Cramp & Simmons 1983), copulated or chased away other Dotterel while remaining close together.

The female's five males were known to be different individuals as one was colour-ringed, one metal-ringed on the left leg, one unringed, one metal-ringed on the right leg and the last was unringed and missing one foot. Only two clutches were found that could definitely be attributed to the female, from the first and fourth of her five pairings. Sheep densities and Dotterel clutch trampling rates were high in the areas used by the

female when with the second and fifth males (pers. obs.), so it is possible that clutches were produced but failed through trampling or other reasons before they could be found. Alternatively, these pairings may have failed to produce a clutch or may have nested outside the study site. This seems unlikely, however, as the timing and duration of pairings were consistent with clutches being laid, and pairs that remain together in an area for several days usually nest in or near the same area (Owens *et al.* 1994). The female was first seen paired on 9 May and last seen on 3 July. As 9 May is the earliest date for clutches to be initiated in Scotland (Smith & Whitfield 1995), the female's first recorded breeding attempt is likely to have been her first of the season. In Scotland, an estimated 4.5% of clutches are laid after she was last seen in the study site (D.P. Whitfield unpubl. data), so there was a possibility of a sixth pairing on a different hill. The female was paired with each male for a minimum of five, six, eight, eight and nine days. The intervals between when the female was last seen paired with one male and first seen with the next were five, nine, two and five days. As the site was visited on only 44% of days between the female's first and last sightings and the female was found on only 63% of visits during this period, these figures probably underestimate the duration of pairings and overestimate the time between pairings. Between her second and third pairings, the female was seen alone in the area she used with the second male so she may have still been associated with him (during laying the male and female sometimes spend long periods out of sight of each other; pers. obs.). Between her fourth and fifth pairings, the female was seen with another female Dotterel. The female was not recorded at either of the two known nests after the clutches were completed. The mean distance between each of the female's nests

\*Correspondence author. Present address: 34 Acre End Street, Eynsham, Oxfordshire, OX29 1PA, UK.  
Email sue@holtcress.freemove.co.uk

or mean pair locations when no nest was found was  $510 \pm 160$  m ( $\pm 95\%$  CL) while the mean distance between all known nests on the site in the same year was  $680 \pm 120$  m. Other studies report distances from 50 to 600 m between the sequential nests of polyandrous female Dotterel (Cramp & Simmons 1983). The female incubated at a biparental nest on the same site in 1997. She returned to the site in 1999 but was not recorded as either breeding or paired, although this may have been a consequence of reduced observer effort (20 days in 1999 versus 52 days in 1998).

The breeding season in the Dotterel's arctic-alpine habitat only allows males sufficient time for one successful breeding attempt (in the only known exceptional case of a male Dotterel reneating after a successful breeding attempt, the lateness of the second attempt gave it a low probability of success; Smith & Whitfield 1995). Males may potentially increase their reproductive output through cuckoldry but it appears to be uncommon in Dotterel (Owens *et al.* 1995). During the same breeding season, a female that does not participate in incubation can pair and, possibly, nest at least five times (females of other members of the genus can lay 4–5 clutches in a season; Cramp & Simmons 1983, Pienkowski 1984). This indicates a large difference between the sexes in potential reproductive rates (Clutton-Brock & Parker 1992): whereas a male's maximum annual reproductive output will generally be three young, a female's may be up to 15 young (clutches rarely exceed three eggs; Cramp & Simmons 1983). Lifetime differences in potential reproductive output between the sexes could be reduced by greater survival of males. There is no indication that male Dotterel survival is greater than female survival (D.P. Whitfield unpubl. data), although measures of adult Dotterel survival are poor due to their low site fidelity (Whitfield

2001). The sexual difference in potential reproductive rates may have resulted in sexual selection for reversed sexual dimorphism in Dotterel (Clutton-Brock & Parker 1992, Clutton-Brock & Vincent 1991).

## REFERENCES

- Clutton-Brock, T.H. & Parker, G.A. 1992. Potential reproductive rates and the operation of sexual selection. *Q Rev Biol* **67**: 437–456.
- Clutton-Brock, T.H. & Vincent, A.C.J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature* **351**: 58–60.
- Cramp, S. & Simmons, K.E.L. 1983. *The Birds of the Western Palearctic*, Vol. 3: *Waders to Gulls*. Oxford University Press, Oxford.
- Kålås, J.A. 1988. Sexual dimorphism in size and plumage of the polyandrous Dotterel (*Charadrius morinellus*): sex roles and constraints on sexual selection. *Can. J. Zool* **66**: 1334–1341.
- Kålås, J.A. & Byrkjedal, I. 1984. Breeding chronology and mating system of the Eurasian Dotterel (*Charadrius morinellus*). *Auk* **101**: 838–847.
- Owens, I.P.F., Burke, T. & Thompson, D.B.A. 1994. Extraordinary sex roles in the Eurasian Dotterel: female mating arenas, female–female competition and female mate choice. *Am Nat* **144**: 76–100.
- Owens, I.P.F., Dixon, A., Burke, T. & Thompson, D.B.A. 1995. Strategic paternity assurance in the sex-role reversed Eurasian Dotterel (*Charadrius morinellus*) – behavioral and genetic evidence. *Behav. Ecol.* **6**: 14–21.
- Pienkowski, M.W. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. *J. Zool. Lond.* **202**: 83–114.
- Pullainen, E. & Saari, L. 1992. Breeding biology of the Dotterel, *Charadrius morinellus*, in eastern Finnish Lapland. *Ornis Fenn* **69**: 101–107.
- Smith, R.D. & Whitfield, D.P. 1995. Reneating by male Dotterel *Charadrius morinellus* after successfully rearing chicks. *Bird Study* **42**: 174–175.
- Whitfield, D.P. 2001. Dotterel *Charadrius morinellus*. In Wernham, C.V., Toms, M.P., Marchant, J., Clark, J.A., Siriwardena, G.M. & Baille, S.R. (eds) *The Migration Atlas: Movements of the Birds of Britain and Ireland*. T & A.D. Poyser, London.

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