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The functions of elongated tails in birds

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ABSTRACT

The functions of the elongated tails of birds have been the subject of much discussion in recent years. It is clear that in some cases the tail represents a sexually selected ornament, playing a vital role in mate choice. However, what is becoming increasingly apparent is that the tail can also play vital aerodynamic roles during flight, and can thus be a result of natural selection. Tail length manipulation experiments carried out during this work have shown that elongated graduated tails have an aerodynamic role during gliding flight. A function in the maintenance of stability (ring necked pheasants (*Phasianus colchicus*) and optimising gliding performance (black-billed magpie (*Pica pica*), thus these elongated graduated tails have been shown to be a product of natural selection. The question of whether correlated evolution occurred between the advent of gliding flight and the graduated tail shape was investigated. It was found that graduated tails did not co-evolve with gliding flight. However, it was shown that graduated tails had correlated evolution with tail elongated. It has been suggested that the forces acting on a triangular tail can be predicted through the application of slender lifting surface theory and the tail being analogous to a delta wing. This would predict that the tail functioned as a consistent lift producing surface. This study considered whether the tail functioned as a lift producer or a control surface. Stereo video of Harris' hawks (*Parabuteo unicinctus)* was used to assess tail function of a triangular tail. However, the results did not provide conclusive evidence for either theory. In this thesis I show that elongated avian tails perform a number of naturally selected aerodynamic roles during flight.

Key words: *Phasianus colchicus*, *Parabuteo unicinctus*, *Pica pica*, aerodynamics, stability, control surface, glide performance, bird flight, comparative analysis, lift production, natural selection, delta wing.

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CONTENTS

CHAPTER 1

Introduction.

“Since ancient times man has watched and envied the flight of birds”

(Brown 1963)

In 1859, Charles Darwin defined natural selection as the preservation of favourable individual variation and the destruction of variation that is harmful (Darwin 1859). To enable an organism to have greater reproductive success or fitness, a trait must give the organism an advantage over others in the population. Darwin also noted that whilst many characteristics of animals could be explained through natural selection, certain features of some animals appeared to be maladaptive, having no obvious survival function. For example, some traits are highly conspicuous and result in an increase predation risk for the individual e.g. three spine sticklebacks (*Gasterosteus aculeatus*) (Moodie 1972). In order to explain these puzzling features possessed by some species Darwin defined another form of selection which depended on the struggle between individuals of one sex, generally males, for the possession of the other sex, rather than on the struggle for existence (Darwin 1859). This type of selection he called sexual selection.

Sexual selection

Darwin stated that the result of sexual selection was fewer or no offspring rather than the death of the unsuccessful. Sexual selection is thus less rigorous than natural selection due to the lack of mortality (Darwin 1859). In 1871, Darwin published 'The Descent of Man, and selection in relation to sex' in which he outlined his theory of sexual selection in some detail. Here, he elegantly defined it as selection depending on the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction (Darwin 1871). Sexually selected traits are often described as dimorphic and have no obvious naturally selected function. They are traits that are selected for, solely in terms of increased mating success (Krebs and Davies 1993). This provides a mechanism by which elaborate ornaments such as the tail of the peacock (*Pavo cristatus)*(Petrie *et al.* 1991) may have evolved. There are currently three main hypotheses proposed to explain elaborate ornaments in animals and the advent of female choice. These main hypotheses are Fisher's runaway selection, Zahavi's handicap hypothesis and Hamilton and Zuk's parasite loading hypothesis.

Fishers runaway selection proposes that trait and preference become associated in offspring, leading to a runaway process of directional selection. A trait becomes progressively more exaggerated until it becomes a hindrance to survival (Andersson 1994).

Zahavi's handicap hypothesis suggests that a conspicuous, costly male trait is targeted by female choice because such a trait indicates high heritable viability. The trait or ornament is an honest signal of male quality because a male survives despite the handicap of the trait (Andersson 1994).

Hamilton and Zuk parasite hypothesis states that ornaments are a signal of parasite loading and parasite resistance (Balmford & Read 1991). "Animals choose mates for genetic disease resistance by scrutiny of characters whose full expression is dependent on health and vigour" (Hamilton and Zuk 1982). Only birds that are in top condition i.e. have a low parasite load, can afford the cost of a bright plumage or a costly elongated tail (Andersson 1994).

Long tails in birds.

Evidence suggests that the main mechanism for selection towards elongated tails in birds is usually mate choice by the female. An elongated tail is defined as a tail that is longer than the bird's body (Balmford *et al.* 1994). In certain species females have been shown to prefer males with long tails, examples include long-tailed widow birds (*Euplectes progne*) (Andersson 1982) and barn swallows (*Hirundo rustica)* (Møller 1994). In recent years, the idea that some elongated tails actually improve aerodynamic efficiency, manoeuvrability and stability have been explored. In some cases natural selection or a combination of natural and sexual selection, may be a more likely explanation for their evolution. Møller (1994) has found barn swallows tail streamers to be sexually selected traits following a number of tail manipulation experiments. The conclusions drawn from Møller's experiments have been questioned in recent studies (Evans 1998; Thomas and Rowe 1997). Aerodynamic analysis has been used to show that the tail streamers have an aerodynamic function, namely that of control in flight, and therefore they could have evolved through natural selection alone (Evans and Thomas 1997; Norberg 1994). It is also possible that a tail originally elongated through natural selection for its aerodynamic function becomes further elongated past the naturally selected optimum through sexual selection (Norberg 1994). The role of aerodynamics in the evolution of the avian tail brings into question the general assumption of the past that elongated tails represent sexually selected ornaments. There has been a need to develop methods of distinguishing between the two potential mechanisms of evolution, natural and sexual selection. Manipulation experiments have been used to provide information on the likely costs associated with an observed trait. A naturally selected structure is predicted to be at a level that maximises the net benefits of that structure. A sexually selected trait is predicted to be at a level that is costly (Evans and Thomas 1997). This suggests that if a structure is a product of natural selection it should be at a level where any deviation leads to an increased cost. A sexually selected structure would be expected to show an increase in cost only if the structure was further exaggerated and a reduction in costs if it were reduced.

The likely mechanism of evolution of an elongated tail in a particular bird species could be considered through the use of tail length modification experiments. If tail length modification was shown to have an effect in terms of aerodynamic costs, the nature and direction of this effect could be used to assess the mechanism behind the evolution of the long tail. If a tail was lengthened as a result of a naturally selected aerodynamic function, an elongation or a reduction in length should lead to a decrease in aerodynamic performance, and an increase in costs associated with flight. If the tail was elongated through sexual selection as a mate choice ornament, any reduction in the length of the tail should lead to an improvement in aerodynamic performance. As the tail approaches a size nearer to the aerodynamic optimum, aerodynamic costs would be reduced. This effect is illustrated in figure 1, with natural selection represented as a U-shaped curve with the minimum turning point being the aerodynamic optimum where costs are minimised. Sexual selection is represented by a sloping line with reductions in tail length leading to decreased costs. A combination of natural and sexual selection would lead to observed tail lengths being extended beyond the naturally selected optimum. This would result in a reduction in tail length initially leading to a decrease in costs until the naturally selected optimum was reached. Subsequent reduction in tail length would lead to costs increasing (Evans and Thomas 1997).

If a tail could be shown to be naturally selected for an aerodynamic role, a completely different set of evolutionary constraints compared to those applied to a sexually selected ornament would be applicable to the structure.

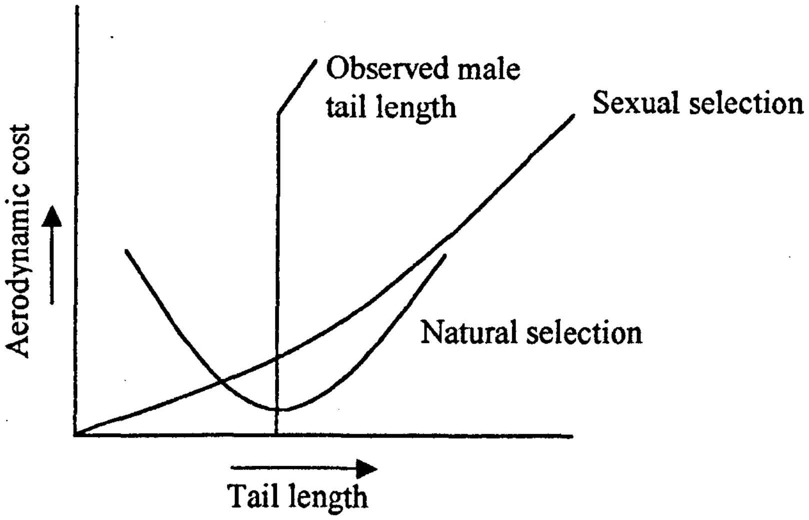

Figure 1. Distinguishing between natural and sexual selection

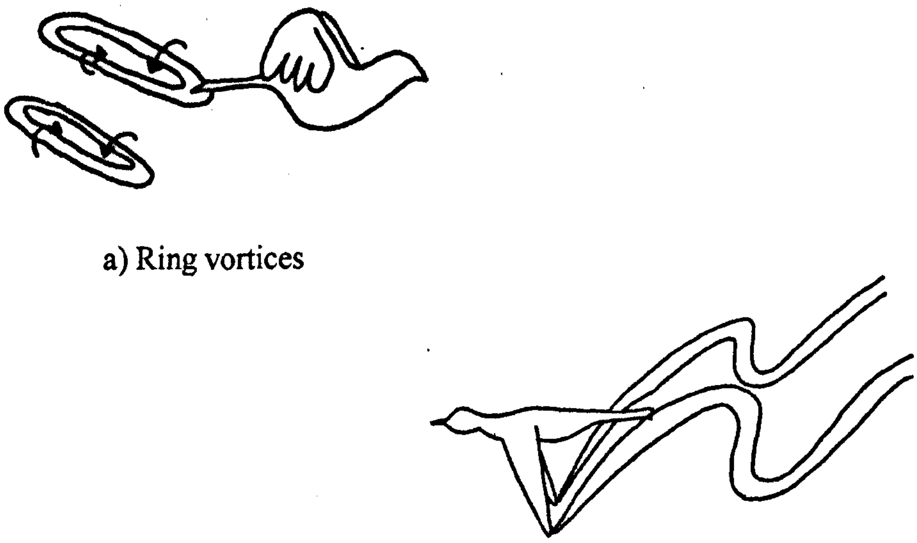

Figure 2. Slow and fast flight trailing vortices.

Bird flight

Bird flight is affected by two major components, drag and lift. Drag is the force acting in the opposite direction to movement and is overcome by thrust (Altringham 1996). Lift is a force acting at right angles to the flow of the fluid (Rayner 1988) and overcomes the effects of gravity (Altringham 1996). The total drag on the bird can be divided into three components, parasite drag, profile drag and induced drag. The three components of drag are defined as follows. Parasite drag is the drag associated with the bird's body. Profile drag is caused as a result of friction as air moves over the wings, and induced drag is a result of lift production (Thomas 1996b). An aerofoil generates lift because, when at an angle of attack in relation to the direction of airflow, air moves more quickly over the upper surface than the lower. Bernoulli's theorem, describes steady flow along a streamline (Alexander 1971) and states that where the velocity of a fluid is high, the pressure is low, and where the velocity is low, the pressure is high. This sets up a pressure gradient and air tries to circulate from the area of high pressure below the aerofoil to the area of low pressure above. The amount of lift and drag generated by the aerofoil depends on its angle of attack (Altringham 1996). The circulation about the wing continues to increase with increasing angle of attack until the airflow becomes turbulent at which point the wing stalls and lift is lost (Altringham 1996). As the air moves around the lateral ends of the wing it gains a certain amount of kinetic energy, this kinetic energy is retained after the aerofoil has passed (Alexander 1971). The retained energy accelerates the air behind the bird downward in a wake, a complex vortex structure in the air (Pennycuick 1989; Rayner 1988). The magnitude of lift that the bird produces in powered flight is proportional to the circulation of the bounded vortex and proportional to the wingspan (Pennycuick 1989). At the wing tip the bounded vortex becomes a trailing vortex (Pennycuick 1989). Trailing vortices can be divided into two broad groups (Rayner *et al.* 1986), those produced by a bird in slow flight (vortex rings) (Spedding *et al.* 1984) and those produced during fast flight (vortex wakes) (Rayner *et al.* 1986). In slow flight, only the downstroke of the wings produces lift (Rayner 1988). The bird's wings move slightly backwards during the downstroke and the bird moves forward. At the end of the downstroke the bird folds its wing in towards its body to reduce drag created by the upstroke, this 'snatches' the wing out of the vortex ring that has just been created (Pennycuick 1989; Rayner 1988). The wing movements in slow flight lead to distinct ring vortices making up the wake (figure 2a) (Pennycuick 1989; Rayner 1988). In fast flight, a continuous ladder-like trailing vortex is formed as the wings remain straighter throughout the up and down stokes creating lift during both movements (figure 2b) (Pennycuick 1989; Rayner 1988; Thomas 1993b).

In gliding flight, a bird produces lift but no thrust. Thus, in steady gliding flight, there is no thrust produced to counteract drag, therefore the bird must decline downwards at some angle (Pennycuick 1989). The most efficient flight comes from a high lift to drag ratio (Thomas 1993b). The lift to drag ratio is reduced by the bird's tail (Thomas and Balmford 1995). However, the avian tail allows birds to exhibit variable flight behaviour. For example, it helps to maintain stability and control the angle of attack of the wings, thus allowing the bird to fly at more than one speed (Thomas and Balmford 1995). Flight represents a very complex form of locomotion. During flapping flight both wing and tail angles, velocities and shapes can change instantaneously (Norberg 1990). This work has concentrated solely on gliding flight to minimise some of this complexity.

The tail

Birds' tails vary far more than their wings (Thomas 1993c). In slow flight, the tail is typically widely spread and lowered to a high angle of attack in relation to the direction of flight (Rayner 1988; Thomas 1993b). As the bird accelerates it gradually reduces the tail's angle of attack, in addition during high-speed flight the tail is furled (Thomas 1993c; 1996a). It has been suggested that the tail has three overall functions. One aerodynamic (Thomas 1993b), one as a signal in sexual selection (Thomas 1993b; 1996b) and one as a mechanical prop (Thomas 1996b). The potential aerodynamic functions of the tail can be divided into three groups. The production of substantial lift in addition to that produced by the birds wings during acceleration, turning and slow flight (Thomas 1993b; Thomas and Balmford 1995), maintaining aerodynamic stability (Thomas 1993c) and controlling the angle of attack of the wings and balancing pitching moments they generate (Thomas 1993c; Thomas and Balmford 1995). The possession of an elongated tail ornament is limited by the bird's power requirement to fly. If the elongated tail increases the minimum power needed to fly above the power available, the bird will no longer be able to fly aerobically. If the ornament increases the maximum range power above the power available the bird would be unlikely to be capable of sustained flight (Evans 1999). The shape of the power curve relating speed and power is affected by bird morphology. The tail's size is particularly important but, in general, if the tail produces lift it has the effect of broadening the bottom of the U-shaped power curve (Thomas 1996a).

Stability

Pennycuick (1975) defined stability as being when a disturbance from equilibrium gives rise to a force or moment that tends to restore equilibrium. It is suggested that the tail seems to have been designed to generate lift during slow flight which stabilises and balances the bird (Hummel 1992; Thomas 1996a; b; Tucker 1992). There seems to be little doubt that the tail performs some stabilizing function during flight (Pennycuick 1975). A bird must maintain stability about three axes, roll (the horizontal and longitudinal axis), yaw (side to side movement on the vertical axis) and pitch (the head up and down motion on the lateral horizontal axis) (Pennycuick 1975). Hummel (1992) implicates the tail in maintenance of pitch stability. Further to this, work by Tucker (1992) on a Harris' hawk flying in a wind tunnel suggests the tail acts as a stabiliser, balancing the pitching moment generated in slow flight. The role of providing stability may represent a function an avian tail could perform even when far from the proposed aerodynamic optimum tail shape for lift production. A graduated tail represents one such tail shape far from this suggested optimum. Whilst not producing substantial lift to actively provide stability, the drag produced by such a tail may passively contribute to stability in a similar way to the feathers on a dart (Alexander 1971; Evans and Thomas 1992; Thomas 1993b). As such, it has been suggested that a graduated tail could represent the most stable tail shape (Thomas 1993b). A bird that flies infrequently could benefit from the passive stability such a tail would provide (Thomas 1993b). This would provide a potential naturally selected function for elongated graduated tails.

Glide Performance

The tails of birds potentially perform a wide variety of aerodynamic functions during flight. These functions may be described directly, for example maintenance of pitch stability or in broader terms, for example enhanced aerodynamic performance. In addition to the potentially stabilising role of an elongated graduated tail, such a tail shape may play a role in a bird's overall glide performance. A fundamental measure of aerodynamic efficiency and performance is glide angle, which is the equivalent of the lift to drag ratio (Thomas 1993c). A bird's glide performance is described as the relationship between sinking speed and forward velocity (Pennycuick 1989). A bird's sinking speed is a product of its lift to drag ratio and as such its glide angle. Glide angle and forward velocity thus provide a useful measure of glide performance. Glide performance could be used to assess whether a bird's naturally observed tail length represented a naturally selected optimum in terms of gliding performance. A naturally selected optimum would implicate the elongated graduated tails as having an aerodynamic function. This would provide further evidence of the tail representing a vital component of bird flight in areas other than straight lift production.

Lift production

The only current theory on how the tail produces forces during flight applies slender lifting surface theory to predict aerodynamic properties and forces acting on a bird's tail (Thomas 1993b). Thomas (1993b) considered the avian tail to approximate to a delta wing. As such it is a separate aerofoil and classic aerodynamic theory can be applied to flow over this slender lifting surface (Thomas 1993b). A delta wing is a basic configuration for supersonic flight. At subsonic speeds the flow separation characteristic of delta wings provides lift and manoeuvrability well beyond what one would expect from a standard aerofoil (Lowson and Riley 1995). The airflow over the tail is highly three-dimensional and is dominated by flow around the edges from below the tail to above it (Thomas and Balmford 1995). The shape of a delta wing is such that two spiralling leading edge vortices are formed as the air moves around the sides of the wing (figure 3) (Gad-el-hak and Ho 1985; Lee and Ho 1990; Rediniotis *et al.* 1994). The lift produced by the wing is thought to be a result of the vortex system (Chang and Lei 1996). Suction footprints are created on the top of the wing that enhance lift (Kumar 1998; Lee and Ho 1990; Norberg 1994). The delta wing represents a good method of obtaining high lift at large angles of attack (Gad-el-hak and Ho 1985). The stationary vortices created due to the slanting leading edge prevent the wing from losing lift and stalling (Lee and Ho 1990). Thomas (1993b) used slender lifting surface theory to produce a model to predict the forces acting on the tail. He made predictions about the effects of different angles of attack and aspect ratios on vortices and also the effects of variation in tail shape and spread on aerodynamic performance. His work suggests that a tail can generate useful lift even when the shape is far from the aerodynamic optimum. In terms of lift production, the optimum tail shape is triangular when spread at 120° and forked when furled (Balmford *et al.* 1993). This is a result of profile drag being proportional to the area of the tail but lift and induced drag being dependent only on the tail's maximum continuous span. Maximum lift for a given drag is produced by a spread triangular tail (Balmford *et al.* 1993; Thomas 1993b; Thomas and Balmford 1995). A tail only generates lift if it increases in width along the direction of flow, so that the mass of air flow around the edges of the tail increases along its length (Thomas 1993b; 1996a; Thomas and Balmford 1995). A tail that has parallel sides only generates drag (Thomas 1993b; 1996a). Graduated tails are not aerodynamically optimal in terms of lift production, because although they generate the same amount of lift as a normal tail, they also generate substantially more drag (Balmford *et al.* 1993). This is a result of any section of tail behind the point of

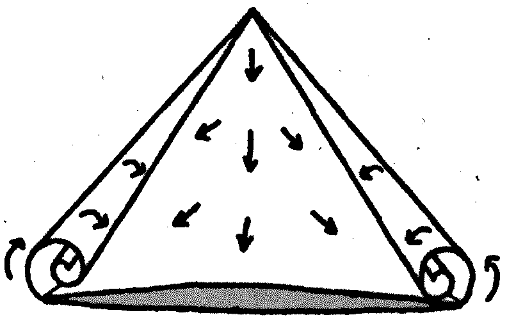

Figure 3. Air flow around a delta wing.

maximum continuous span, where tail width is decreasing, producing drag and not lift (Lee and Ho 1990; Thomas 1993b; Thomas and Balmford 1995). The outer tail feathers produce the majority of lift created by the tail (Evans and Thomas 1997; Thomas 1993b). A bird that can droop its outer tail feathers to generate leading edge suction can reduce the induced drag by half (Evans and Thomas 1997; Lee and Ho 1990; Thomas 1993b). Norberg (1994) put forward the idea that tail streamers could act as control devices forming vortex flaps to generate lift. Thus, tail streamers will have differing aerodynamic parameters to graduated tails even when they are the same size (Evans 1999). The Norberg mechanism cannot operate when tail streamers are not present and only operates during turns (Evans and Thomas 1997). The magnitude of this effect depends on the length of the tail streamers (Evans 1999).

A further complication to the aerodynamics of the tail is added through asymmetry. An asymmetric tail can cause both loss of lift and an asymmetric distribution of lift. Asymmetry can thus lead to a reduction in manoeuvrability (Thomas 1993). A considerable sideways force can result when a tail is tilted to some angle of roll that actively creates vortex asymmetry, such forces would provide the ability to control turns (Thomas 1993b). A tail of asymmetric shape produces yaw and roll moments during straight flight. In order to compensate for this, the bird must rock its tail utilising the forces produced. This ultimately reduces manoeuvrability because it reduces the amount the bird can tilt its tail to create turning forces, the only rock available being that which is left after the bird has compensated for the yaw and rolling moments created by the asymmetric tail (Thomas 1993a).

Thomas's theory of tail function remains the only explanation of how the tail produces lift during flight. Work on starlings (*Sturnus vulgaris*) using wind tunnel experiments has been carried out to begin to test the validity of the model and its assumptions (Maybury *et al.* 2001). However, no work has yet been carried out on birds in free-flight.

Is a bird's elongated tail purely a product of sexual selection? Or does it provide some other survival function and thus be either partially or wholly a product of natural selection? In some species, such as the ring-necked pheasant, the evidence that the tail has elongated through sexual selection is equivocal. It is possible that tail elongation in this species and for example the black-billed magpie has occurred as a result of an aerodynamic function they perform. The avian tail's functions in mate choice and aerodynamics indicate a complex relationship involving trade-offs between various tail functions and the bird's ecology. The bird's ability to alter its tail shape and span mid flight make its aerodynamics far removed from modern aircraft.

Is the view that elongated tails are a result of sexual selection through mate choice a simplistic one? It has already been shown that some birds' tails perform subtle aerodynamic roles such as increasing manoeuvrability. Should we be readdressing the broad assumptions that many bird species have tails elongated through sexual selection and begin looking for other potential functions for elongated tail?

Does the birds' tail really function as a delta wing as Adrian Thomas suggests or are we still in the position of having no fundamental theory on how the bird's tail functions during flight.

Aims of study

This study aims to begin to address some of the questions associated with the avian tail and to consider the possibility that some tails are a result of natural selection rather than sexual selection. Experiments were undertaken on three different bird species and a literature based comparative analysis was carried out.

Ring necked pheasant *(Phasianus colchicus)*

It has been suggested that elongated graduated tails play a stabilising role during flight. This would suggest that the present tail morphology could be a result of natural selection for aerodynamic considerations rather than sexual selection for mate choice advantage. A tail length manipulation experiment was carried out on model pheasants to investigate this potential tail function. The results of this experiment are presented in Chapter 2. Following on from this experiment the intention was to consider the same questions on live pheasants in free flight. This was to be done using stereo video techniques and would have allowed the inclusion of behaviour and body movement excluded by the use of model birds. The experiment preparation and fieldwork was carried out over a six-month period. Birds were reared in captivity from 6 weeks old to full plumage. Following approximately 60 hours of field experiments the experiment was abandoned. This was due to an inability to control the direction of flight of birds, the success rate of obtaining video footage was <10%. For every 100 birds released less than 10 flights were filmed of a standard that could be used.

Black-billed magpie *(Pica pica)*

Work presented here on model pheasants provide the first evidence of elongated graduated tails performing an aerodynamic role. However, the nature of the experiment was such that it only represented a first step toward investigating a naturally selected role for this tail shape. Following the difficulties experienced with live pheasants an experiment was undertaken on a member of the Corvid family. The family is well known for their intelligence and ease of training. Magpie chicks were reared from about 20 days old to full plumage in an outside aviary. Tail manipulation experiments were carried out following the post fledgling moult to assess the effects of changing tail length on glide performance. The results of this work are presented in chapter 3. It was felt that the combination of the two techniques, model birds and live bird flight experiments, would provide a two pronged approach to addressing the question of whether elongated graduated tails could be implicated as having an aerodynamic role.

Correlated evolution

The possibility of graduated elongated tails performing an aerodynamic function during gliding flight provides a mechanism through which natural selection may elongate tails. If graduated tails are in general selected for by an aerodynamic role rather than by a mate choice function, they may play a fundamental role in bird flight. Such a role would suggest that the evolution of graduated tails and the advent of gliding flight in a species might be correlated. Comparative analyses search for evidence that traits have co-evolved by considering the current form of each trait across a number of species. Ancestral states are then estimated and the likelihood of correlated evolution assessed. A comparative analysis controlling for phylogeny was undertaken to investigate the likelihood of gliding flight being correlated with graduated tail shape in species from the Order Aves (Chapter 4).

Harris' hawk (*Parabuteo unicinctus*)

In order to address issues raised by Thomas's (1993b) theory of the forces acting on the birds tail detailed information on bird movements during flight would be required. Predictions made from Thomas's model could then be used as a starting point for an investigation into how the birds' tail functions during gliding free flight. A stereo video technique was used to obtain reconstructed three-dimensional flight paths. This allowed calculations to be made regarding bird movements. Large, slow moving birds needed to be filmed at close range to obtain the necessary information. Harris' hawks, a widespread falconry bird in the UK provided an ideal candidate for the study. A number of other species were filmed in the wild including common buzzard *(Buteo buteo)* and black headed gulls *(Larus ridibundus)*. However, the quality of footage obtained and the inability to identify individual birds moving in a flock made the use of Harris' hawks the final choice of species for the study (chapter 5).

The overall objectives of this work were to investigate the roles of the avian tail during flight. Is the avian tail naturally selected to perform aerodynamic functions such as increased stability or sexual selection for a mate choice advantage? Assuming the tail does function during flight what specific roles do different tail shapes play?

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CHAPTER 2

A naturally selected role for the elongated tails of ring necked pheasants.

INTRODUCTION

Elongated tails of birds are often used as examples of sexual selection. Evidence suggests that one mechanism for selection towards elongated tails is mate choice by the female. In some species females have been shown to prefer males with longer tails, two classic examples of this are the long-tailed widow bird (*Euplectes progne*) (Andersson 1982) and the barn swallow (*Hirundo rustica*) (Møller 1994).

The ring necked pheasant (*Phasianus colchicus*) (Plate 1) is a ground dwelling game bird. Both male and female pheasants have elongated graduated tails, in which the central tail feathers are the longest with feathers gradually decreasing in length away from the centre. Typically, a pheasant's flight consists of rapid wing beats followed by a gliding phase towards landing. They have the ability to take off vertically to escape predators (Rayner 1979) but rarely fly for long distances (Cramp 1987). Pheasants are highly dimorphic with males exhibiting a number of traits that are probably sexually selected and which have been the subject of several studies of mate choice. Mateos and Carranza (1995) found that females preferred males with elongated tails, black points on the wattle and elongated ear tufts. However, the main focus of most other studies has been the leg spurs and their potential role as a sexually selected trait. Two studies of a wild population of Swedish pheasants have indicated that spur length plays an important role in female mate choice. Görransson et al. (1990) found spur length to be the most important predictor of harem size, while Wittzel (1991) showed that spur length was the most important factor in male reproductive success. However, Hillgarth (1990) studying captive birds in Britain found no female preference for longer spurs (Hillgarth 1990). In addition to this, Mateos and Carranza (1995) studying captive birds found no support for the hypothesis that spurs play a role in female mate choice.

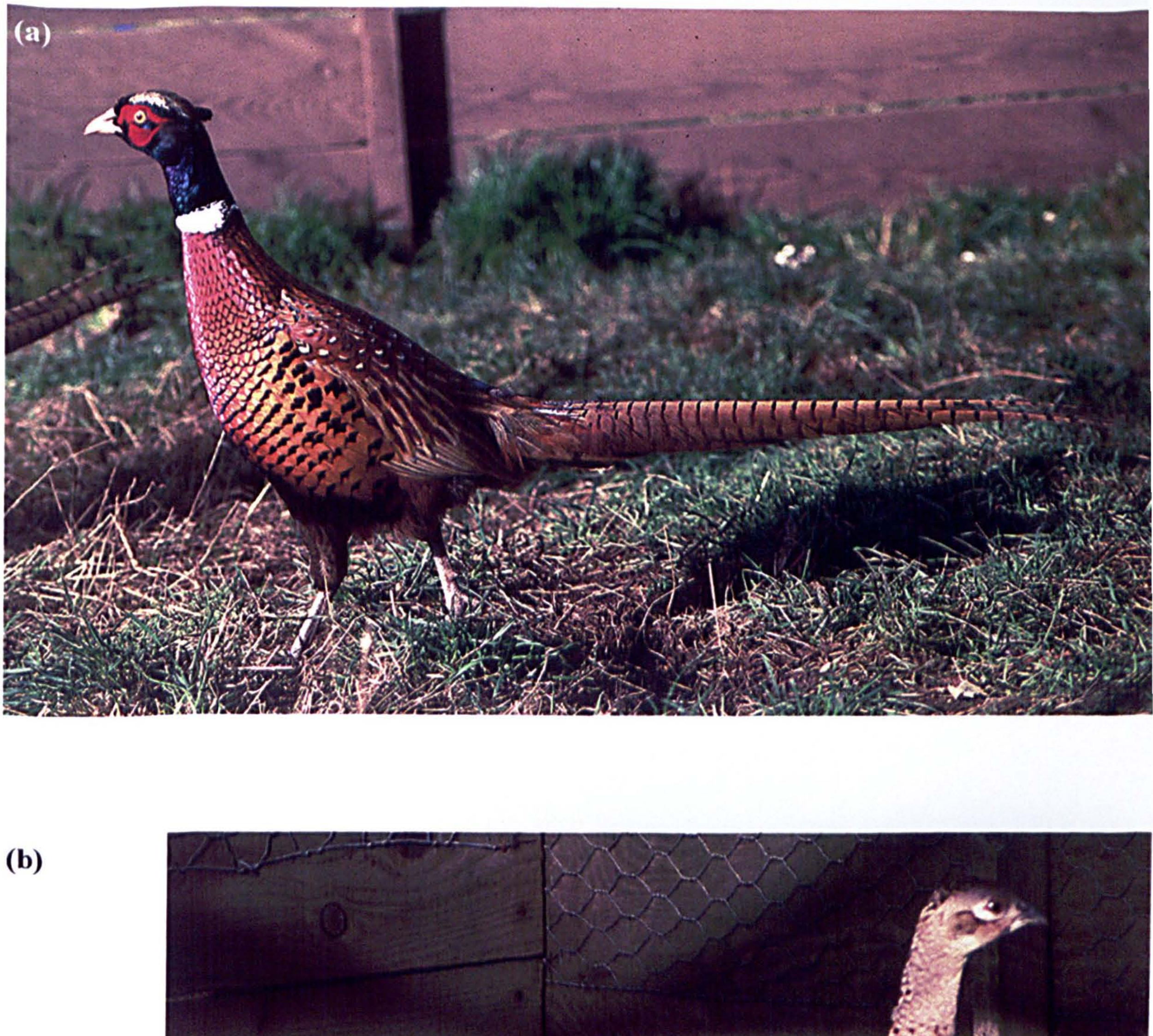


PLATE 1. Ring necked pheasant (*Phasianus colchicus*) (a) male and (b) female

It is clear that sexual selection in the ring-necked pheasant is a complex issue. In a review paper, Mateos (1998) suggests that the reproductive success of male pheasants is a result of a complex suite of characters that together produce differences between males, as such it is difficult to determine the selection pressures resulting in any given trait. The difficulties faced when trying to understanding specific roles for specific traits in the pheasant are again seen when considering their elongated tails. Pheasants have an elongated, graduated tail that is kept all year round (Cramp 1987). The condition of the bird's feathers does not appear to convey information about the physical condition of an individual during the mating season as the moult takes place post-breeding (Mateos 1998) although feather wear could. The male uses his tail during courtship (Cramp 1987) and the tail has been shown to be important in male-male competition and displays (Schantz *et al.* 1989); (but see (Mateos and Carranza 1995)). Tail length has been shown to be used as a cue by females during mate choice (Geis and Elbert 1956; Mateos and Carranza 1995); (but see (Göransson et al., 1990)). However, a study of a feral population in Sweden, considering directional selection of morphology, found no effect of tail length on male reproductive success (Wittzell 1991). The evidence that the tail is purely sexually selected thus remains equivocal. Another argument against a simple sexually selected origin for the long tail is that female ring-necked pheasants also have an elongated tail similar in shape but shorter than that of males, if an elongated tail is defined as a tail which is longer than the bird's body (Balmford *et al.* 1994). We suggest that it is possible that the tail may play a non-sexually selected role in females and/or males, and that this effect may explain some or all of the observed elongation.

In recent years, the idea that some elongated tails actually improve aerodynamic efficiency, manoeuvrability and stability have been explored. Such an aerodynamic function would provide a mechanism by which tail elongation could occur through natural selection. Theory suggests that the aerodynamically optimum tail shape for lift generation is a tail which forms a triangle when spread at 120° (Thomas 1993). According to this theory, tails that are long and graduated would generate the same amount of lift as triangular tails, because the lift generated is determined by the tail's maximum continuous span. However, they would also produce substantially more drag, the central feathers extended beyond the maximum continuous span increase the tail's area, and thus drag production, whilst producing no lift (Balmford *et al.* 1994; Lee and Ho 1990). It is possible that a graduated tail, while not an optimum tail shape for lift generation according to an analysis of the lift/drag ratio, may represent a naturally selected optimum for some other function during flight. Natural selection may favour a design of tail that is optimal in terms of many potential aspects of flight performance, which one predominated would depend on the ecology of the species concerned. Birds that fly infrequently or have a gliding phase of flight may benefit from a tail that performs a function other than lift production.

Tucker (1992) suggested, from an analysis of a Harris' hawk gliding in a wind tunnel, that the tail could act as a stabiliser balancing pitching moments. In the gliding phase of flight a passive stabilising role for a graduated tail could be envisaged in which the tail dampened pitching moments induced by the wings. If such an aerodynamic role could be shown, a mechanism for elongation other than sexual selection would have been found. Analysis of costs related to flight can be used to distinguish between natural and sexual selection as mechanisms of evolution. A structure that is naturally selected is predicted to be at a level which maximises the net benefits of the trait (Evans and Thomas 1997). Therefore manipulations that take the structure away from its current size will be deleterious.

In this case natural selection can be implied if tail manipulations to increase and decrease tail length can be shown to decrease stability.

The aim of the present study was to investigate a potential stabilising aerodynamic role for the pheasant's elongated graduated tail during gliding flight. Is the tail of the male pheasant a product of sexual selection, or is the elongated tail of both males and females an optimum for some other function. A naturally selected function for the pheasants' elongated tail would provide an evolutionary mechanism for the elongation of both male and female tails in this species.

MATERIALS AND METHODS

Model Pheasant

In the autumn of 1998 and 1999 dead pheasants were obtained from local estates following annual shoots. Biometric measurements of each bird were taken, these were left and right wing length (maximum wing chord); and length of six central tail feathers measured to nearest millimetre with a ruler from the uropygial gland to the tip of the feather; right and left tarsus to nearest 0.1 millimetre with callipers; body mass was measured to nearest 20g using a pesola spring balance. Paired measurements were averaged to calculate mean wing length and mean tarsus. Only birds in good condition with no external damage were used. The internal organs of each bird were removed and discarded. Expanding insulator foam was injected into the body cavity to maintain the overall body shape of the bird and formaldehyde was used to preserve the birds. When injected into the muscles, formaldehyde has the effect of both preserving the tissues and making it rigid. The bird could thus be preserved in a glide position as once dry the bird maintains the shape it is set in prior to injection. A glide position was defined as the wings at full stretch and tail spread to its full natural extent (see figure 1a).

Experimental frame

A frame was designed to carry the bird above a Toyota Hi-lux pick-up to allow the experiment to be carried out over a range of air speeds. The frame consisted of two vertical poles positioned 620mm apart on a frame above the cab of the vehicle. Each vertical pole had a horizontal screw threaded rod 320mm in length, 10mm from the top, these held the bird in position. The bird was thus held at 520mm from the base of the frame on the top of the cab. It was held in position by spikes on two discs either side of its body at the end of each horizontal rod. The disc rotated freely on ball races in the fixing to the frame. This arrangement allowed free rotation through 360° on the pitch axis. The bird was mounted on the frame on its centre of mass, with the horizontal rod perpendicular to the long axis of the bird. The experimental frame is illustrated in figure 1b. The frame also allowed a camera to be attached to the vehicle 1850mm behind the bird to allow bird movements to be filmed.

Time to stability

The experiment was carried out on clear, still days when the air speed was less than 1.5 m/s. During the experiment the vehicle was driven at five different air speeds 5.6, 6.9, 8.3, 9.7 and 11.1 m/s. Other work suggests initial flight speeds for pheasants of 7.76 m/s for male and 6.49 m/s for female (Bagliacca *et al.* 1996). The air speed was the speed of the air flowing over the model bird. This was measured using an anemometer (AV competition, Brauniger flugelectronic, Wilhelm, Germany) that consisted of the speed detector and an electronic reader. The speed detector was attached to the frame to the right of the model bird, a wire attached the detector to the electronic reader that was kept inside the vehicle, thus the air speed at the model could be read on an electronic display inside the vehicle.

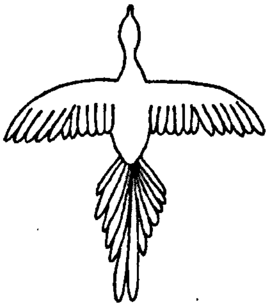
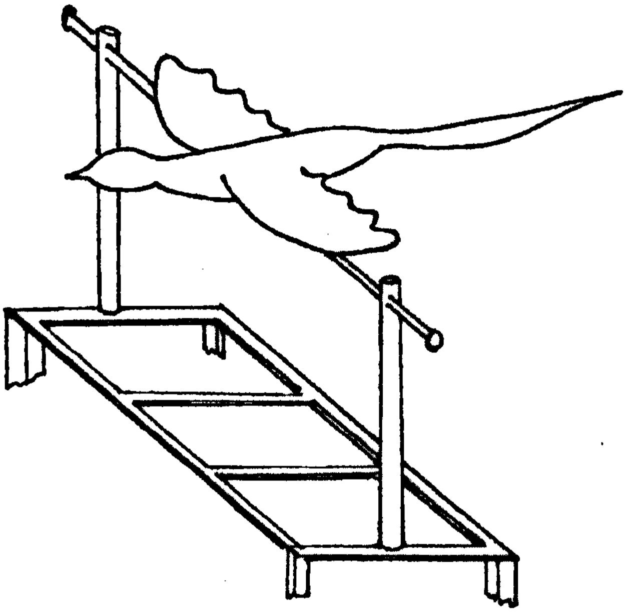


Figure 1(a) Position of wings and tail in a preserved gliding pheasant.



(b) Experimental frame with model pheasant

At each air speed the bird was allowed to reach and maintain a stable horizontal glide. It was then deflected from this position by pulling its head downwards. This caused the bird to undergo a series of oscillations until its original glide position was regained. The depth of the downward deflection was found not to have a significant effect on the time taken to return to the original glide position ($F_{1,27}$=0.85, p=0.365). The stability of the bird was determined by measuring the time it took for a model pheasant to return to the initial glide position following downward deflection.

The experiment was filmed using a Panasonic palmcorder NV-S85 to allow the time taken to return to the glide position or 'time to stability' to be calculated. The video footage was edited to select the frames of interest using Adobe Premier 4.2 on an Apple Macintosh 9500. NIH Image (available on the Internet at http://rsb.info.nih.gov/nih-image/) was used to find the position of the bird in two-dimensional space over time. The lower edge of the right wing where it joins the bird's body was used to trace the movement of the body. This represented a point on the bird that could be seen clearly throughout the oscillation of the bird and was not subject to movement other than that being measured. From analysis of video footage, a trace of the bird's vertical movement over time was obtained by calculating the distance between the fixed point on the bird and a fixed point on the frame. The fifty position values of the trace before the bird was deflected represented the bird in its glide position. These first fifty values were used to define stability. A regression line was fitted to the position data of the stable phase and the residual of the regression used to calculate 95% confidence intervals. The 'time to stability' was then calculated from the time when the trace of the bird's position crossed the mean of the first fifty values, on the upward movement, to the time when 10 consecutive values of the bird's position fell within the 95% confidence bands defining stability. Time to stability was calculated blind to the tail length manipulation group. Time to stability was found for each bird at each air speed and tail length combination, each combination was tested twice and an average calculated. The repeatability of the time to stability was estimated as 42% ($F_{30,47}$=2.43, p=0.001) (Lessells and Boag 1987).

Tail manipulation

Each bird was assigned to four tail length categories:

- Control 1. – Natural tail length, tail un-manipulated.
- Control 2. – Natural tail length, manipulated control (tail cut but overall length un-changed).
- Two tail length modification groups.

In the tail length modification groups, birds were randomly allocated to two of six possible tail length changes, an increase or decrease of 1,1.5 or 2 standard deviations calculated from a natural population (R. Draycott, pers.com.). Male and female tail length distributions were calculated independently (1 s.d. female 34mm, 1 s.d. male 85mm). The six central feathers of the tail were subject to manipulation. Tail manipulation was achieved by removing the feather tip, removing or adding the required length of tail and reattaching the original tip, thus maintaining the tail's natural shape. Feathers were reattached by inserting a 10mm length of wire (1mm gauge, <50mg) into the shaft of the feather and securing with cyanoacrylic superglue (Perma Bond, National Starch and Chemical. UK). This series of manipulations meant that each bird acted as its own control so that differences between treatments were due to the differences in tail length rather than differences between models.

Air flow over vehicle

An experiment was carried out using a 1/3 scale model of the vehicle used in the experiment. The model was made out of a polystyrene block which was painted with emulsion after shaping. The model was placed in an open circuit wind tunnel, the angle of air flow in relation to the roof of the vehicle and air speed were measured.

Angle of air flow.

The air flow over the vehicle was visualised by injecting smoke streams into the air flow over a range of wind speeds from 7.3 to 17.4 m/s (equivalent to 2.4 to 5.8 m/s during the field experiment, a 1/3 scale model must be tested at 3x actual speed (pers.com. R Galbraith). Video footage was taken using a Sony digital camera (Sony Digital Handycam DCR-VX1000E), and edited using Adobe Premier 4.2 and NIH image as described above. The mean angle of the smoke from the horizontal was –1.5 degrees with a range from –4.29 to 2.04. Increasing air speed showed no systematic difference in angle from the horizontal.

Turbulence intensity

Air speed was measured at the point at which the model bird was mounted above the vehicle (20cm above roof) in two positions, at the front and back of vehicle cab. Twenty measures were taken at 10-second intervals for three air speeds in the two positions. The turbulence intensity was measured as the residual of the air speed, expressed as a percentage of the mean air speed (this measure is also known as the root mean square (RMS) wind speed fluctuation) (Pennycuick *et al.* 1997). Turbulence intensity was found to be between 0.6 and 1.3% with lower turbulence intensity values at the higher air speeds. Air speed was found to increase by a maximum of 0.2m/s from the front of the cab to back.

Statistical analysis

Due to the presence of repeated measurements on individual birds in the experimental design the data has been analysed in two different ways which both control for the repeated measures. The two methods undertaken were 1) General Linear Model (GLM) using Minitab release 12.1 where the error term was adjusted to take repeated measures into account. 2) Residual Maximum Likelihood (REML) using Genstat release 4.1.

1) GLM analysis

Initially air speed, manipulation size, manipulation size^2, weight of whole bird and maximum tail length were included in the model as continuous independent variables (covariates). Sex, manipulation technique (effect of cutting and reattaching feather) and an individual bird code were included in the model as factors. The dependant variable was time to stability. Also included were interactions between each of the factors and covariates with individual bird. Model simplification through step-wise elimination of non-significant independent variables was undertaken. The residuals of the data were checked for normal distribution and homoscedasticity at each stage. As a result of checks to ensure the assumptions of the model were met, the time to stability data were Log_{10} transformed to normalise the distribution. Manipulation technique and individual bird were constrained within the model regardless of their significance. The final GLM model included air speed, manipulation size, manipulation size^2, manipulation technique, individual birds and interactions between each factor and individual bird to control for repeated measures. The use of repeated measures has the effect of inflating the denominator degrees of freedom. To control for the use of repeated measures the denominator used to calculate F was the adjusted mean squares for the interaction between individual and the factor of interest rather than the error adjusted mean squares as in a conventional ANOVA. This reduces the denominator degrees of freedom to the number of birds rather than the number of samples.

2) REML analysis

A REML analysis was carried out with fixed effects of air speed, manipulation size and manipulation size^2. Individual bird was included in the model as a random effect. The time to stability data was Log $_{10}$ to normalise the data. REML can produce estimates of the amount of variability due to random effects such as individual bird (Horgan and Hunter 1993). The residuals of the data were checked for normal distribution and homoscedasticity. The significance of the terms was determined using the Wald statistic which is distributed as a chi-square. The effects of individual bird, manipulation technique, weight, maximum tail length and sex were found to be not significant and were left out of the model.

The coefficients from the GLM model were used to produce an equation to calculate predicted values for time to stability at different air speed. The minimum point of the curvilinear relationship between time to stability and manipulation size was found by differentiation. The minimum point on a curve (i.e. the manipulation size at which the rate of change of the function becomes zero) can be defined as df/dx=0. Bootstrapping was used in S-plus 4.5 to generate a population of minimum points from the original data set. This allowed 95% confidence intervals for the turning point to be calculated.

RESULTS

The time taken to return to stability was found to increase when the tails of both male and female pheasants were increased or decreased away from the individual's naturally observed tail length. The Log$_{10}$ time to stability for each bird presented as a mean of all air speeds at the four allocated manipulation lengths is show in figure 2. The data set included 12 individuals, 6 males and 6 females. The figure indicates

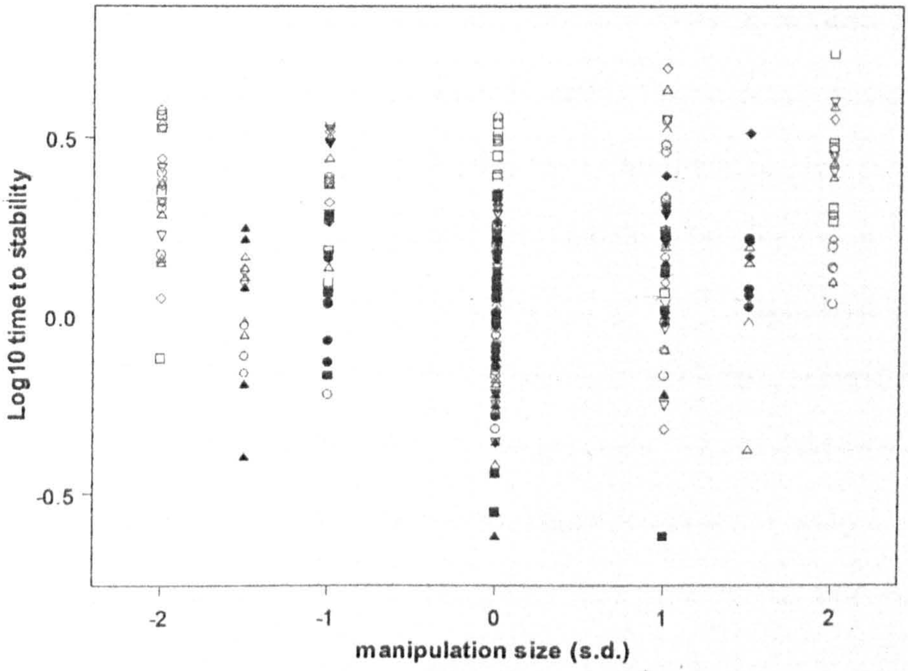


Figure 2. Log_{10} time to return to stability following deflection (time to stability) for male and female ring-necked pheasants with different tail lengths, air speeds combined. Each bird represented by a different symbol (n=12).

an overall U-shape of the data with longer and shorter tail lengths showing an increased length of time to return to stability. The data was analysed using two different statistical methods, GLM and REML as described above. The two different methods of analysis employed due to the presence of repeated measures in the experimental design in the main gave similar results (table 1). In both cases manipulation size^2 was significant, this describes a quadratic function or a U-shaped curve. Also found to have a significant effect on time to stability was air speed. The analysis indicated that as air speed increased time to stability decreased. In both analyses there was no significant effect of maximum tail length, manipulation technique, weight or sex of the bird. The analysis using a GLM did find a significant effect of individual bird ($F_{11,1}$ 1.89, $p=0.043$) but this was not found by the REML analysis. Some individual bird effect might be expected with birds from two different years being used in the experiment and each individual bird having varying maximum tail lengths and weights. The coefficients from the GLM analysis were used to calculate fitted values for time to stability over a range of tail lengths and air speeds. The fitted values reiterate the U-shaped curve indicated by the data. Increasing or decreasing tail length led to an increase in the time to stability. Increasing air speed led to a decrease in the time taken for the bird to return to stability (figure 3). A population of minimum points of the curvilinear relationship was generated through bootstrapping which allowed turning points for male and females to be calculated independently. The 95% confidence intervals around the turning points were then calculated. Male pheasants had a median minimum of 0.0002 s.d. while females had a median minimum of -0.00025 s.d. The calculated confidence bands for both sexes span zero, which represents the naturally observed tail length (figure 4), suggesting that the minima were not significantly different from zero. The power of the experiment was calculated at 99%, with an effect size

factor	df	adjusted F	p
air speed	1	23.81	**0.000**
manipulation size	1	0.77	0.296
manipulation size^2	1	3.94	**0.031**
individual bird	11	1.89	**0.043**
manipulation technique	1	0.67	0.334
error	201		

Table 1 (a). ANOVA of the effects of manipulation size, manipulation size^2, air speed, individual and manipulation technique on Log_{10} time to stability.
(Due to the repeated measures from individuals, the error term was adjusted, thus the error terms are the adjusted mean squares for (individual * each factor) calculated as adjusted Mean squares factor/adjusted mean squares (individual * factor) and thus having 1 and 11 degrees of freedom.)

factor	df	Chi sq.	p
air speed	1	25.86	**0.000**
manipulation size	1	0.08	0.782
manipulation size^2	1	30.17	**0.000**

(b) Results of REML analysis using Genstat (Log time to stability = air speed + manipulations size + manipulation size^2)

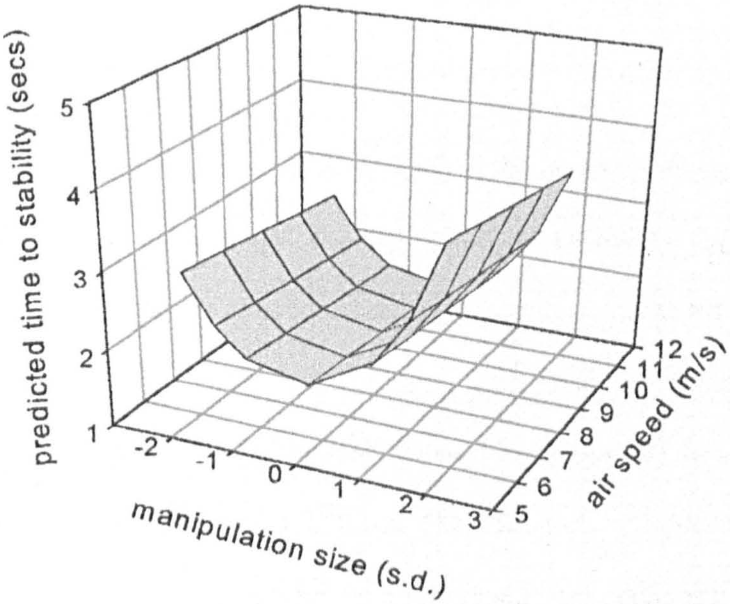


Figure 3. Predicted time to stability of ring-necked pheasants with different tail lengths at different air speeds (predictions calculated from coefficients of GLM).

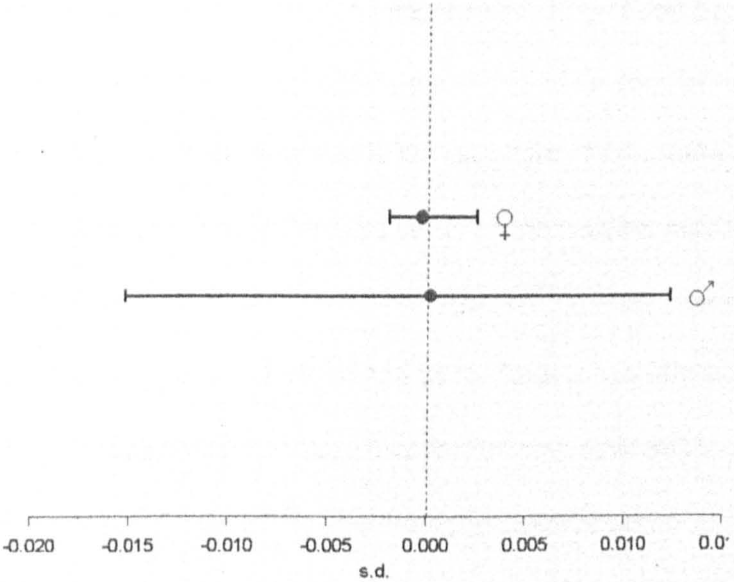


Figure 4. Minimum median turning point values for male and female pheasants with 95% confidence intervals generated from a population of minimum values of curvilinear relationship created by bootstrapping.

of 0.27 using nQuery version 2.0 (Statistical Solutions Ltd. Ireland) suggesting that the effect size and sample size are large enough to avoid a Type II error.

DISCUSSION.

The results suggest that the elongated graduated tail of the pheasant plays a role in stabilising the bird during gliding flight. Increasing and decreasing the tail length, away from that which is naturally observed, leads to an increase in the time it takes for the bird to return to stability following deflection. This result was found by both of the two different methods of statistical analysis used to analyse the data, which contained repeated measures on individual birds. The minimum calculated for the curvilinear relationship indicated that both male and female pheasants had turning points near to zero. Confidence intervals spanned zero indicating that the natural length was near to optimum for pitch stability. I suggest that the naturally observed tail length represents an aerodynamic optimum in terms of pitch stability in gliding flight for the pheasant. The results of the experiment suggest that the pheasants' tail may be a result of natural selection. The flight style and ecology of this species may have favoured a bird that was more stable during gliding flight, rather than one that produced the maximum lift possible. Maximum lift production may sacrifice stability, tails that produce maximum lift and thus have greater manoeuvrability, such as forked tails, have been suggested to be the least inherently stable tail shape (Thomas 1993). It is also possible that other factors may have influenced the evolution of the tail of the pheasant. The cluttered environment favoured by the species may have led to the need for a tail shape the aerodynamic efficiency of which was not greatly affected by damage to outer tail feathers. The lack of sustained flight exhibited by this species possibly removes the need for high lift production by the tail. An aerodynamic function of stability for the tail rather than a mate choice ornament could explain the equivocal evidence in support of the pheasants' tail as a mate choice signal.

The elongated graduated tail of the pheasant may have evolved to compensate for the effects of the development of other traits through sexual selection, for example, increased body size in males. This could explain why the males have significantly longer tails than females. The greater body size of males could have led to a greater elongation of their tails in order to optimise stability. If this effect was non-linear it could lead to males having longer tails than predicted by body weight. This would help to explain why both the male and female naturally observed tail lengths represent the optimum for stability in each sex.

Finally, while the results of this experiment provide evidence for a naturally selected, aerodynamic role for the pheasants tail, other factors should be taken into consideration. It should be acknowledged that there are limitations associated with the use of model birds. The influences of body movement and behaviour on birds in flight should not be overlooked. In order to assess the effects of these factors, live birds would need to be used in an experiment to assess stability during free flight with a range of different tail lengths. It would also be valuable to investigate whether a stabilising function for an elongated graduated tail can be applied to other bird species or whether this role is solely applicable to the pheasant.

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CHAPTER 3

The effects of tail elongation and reduction on gliding performance in the Magpie (*Pica pica*).

INTRODUCTION

The elongated tails of some bird species provide some of the classic examples of sexual selection in the literature. Such examples include the long tailed widow bird (*Euplectes progne*) (Andersson 1982)and the barn swallow (*Hirundo rustica)* (Møller 1994). However, the tail may also play an important role during flight. An aerodynamic function for the tail would provide a mechanism through which natural selection rather than sexual selection could operate. Previously tail elongation in birds has been considered to be purely a result of sexual selection. However, tail length may have increased at least partially through natural selection to increase manoeuvrability, for example in the barn swallow (Buchanan and Evans 2000). Recent work manipulating tail lengths of model ring-necked pheasants (*Phasianus colchicus*) suggested that the graduated elongated tail plays a role in pitch stability during gliding flight (chapter 2). This role may be to passively stabilise the bird in a way analogous to the feathers on a dart (Alexander 1971; Evans and Thomas 1992). Maybury and Rayner (2001) suggest that furled tails function as a splitter plate and wedge playing an important role in minimising drag during flight. Wind tunnel experiments carried out on frozen starlings (*Sturnus vulgaris)* indicated that tail removal leads to a sizable and permanent increase in drag.

The prevalent contemporary aerodynamic theory of avian tail function applies slender lifting surface theory to the tail and suggests that the tail may function in a way analogous to a delta wing (Thomas 1993). The theory states that the airflow around the avian tail is highly three-dimensional and the amount of lift produced is determined by the tails' maximum continuous span. When a tail increases in width down its length at an angle of attack in relation to the direction of airflow, mass is accelerated into the airflow, the acceleration of the air is downward and thus produces lift. The theory predicts that the optimum tail shape for lift generation is a forked tail, that forms a triangle when spread at 120°. The least aerodynamically efficient tail shape in terms of lift production would be an elongated graduated tail (a tail with feathers increasing towards a maximum length in the centre) (Thomas 1993). An aerodynamic function need not be solely lift production; a bird's ecology and behaviour may have led to the evolution of a tail that filled some other role. Magpies (*Pica pica*) have elongated graduated tails. Males and females are monomorphic (Kavanagh 1988) and as such both exhibit what could be classed as a sexually selected ornament in the form of their elongated tail. Their tail has been described as having a function in both territory defence and pair bond formation (Cramp and Perrins 1994). Birds exhibit tail flirting (tail rapidly flicked upwards), tail quivering (tail lifted above horizontal and feathers vibrated) and tail spreading (Cramp and Perrins 1994). It has been suggested that in some monogamous birds mutual sexual selection by mate choice may lead to the development of similar display structures in both sexes. An example of this is the ornamental crest feathers of the crested auklet (Jones and Hunter 1993). Fitzpatrick and Price (1997) suggest that tail elongation in the magpie may have evolved through discriminatory mate choice by both sexes. They found that tail damage was an honest indicator of magpies' reproductive potential and suggest that their results are consistent with the tail having a role in mate choice (Fitzpatrick and Price 1997). However, it is also possible that the magpies' tail performs a naturally selected aerodynamic function. Magpies have a variable flight mode that consists of periods of low-amplitude wing beats interspersed with brief glides (Boggs *et al.* 1997). I suggest that during the gliding phase of flight the tail may represent an optimum in terms of glide performance.

Gliding flight occurs when no propulsive power is provided by the bird's muscles (Pennycuick 1968). In a steady glide a bird produces no thrust to counteract drag and so the flight path must decline at some angle (Pennycuick 1989). A bird's aerodynamic performance in a glide is described by the relationship between a bird's sinking speed and its forward speed. This relationship is called a glide polar (Pennycuick 1989; Tucker 1987; Tucker and Heine 1990). A bird's sinking speed will be related to the angle at which it glides. A bird's forward velocity and glide angle can therefore be used as measures of a bird's glide performance. It follows that there will be an angle from the horizontal below which a bird cannot glide without resorting to flapping flight. I predict that if the tails of magpies are naturally selected to optimise gliding flight then the naturally observed tail length will represent an aerodynamic optimum in terms of the minimum glide angle. As minimum glide angle will inevitably change with forward speed, it is necessary to consider the area under the glide angle – forward speed function, which represents the region of parameter space in which the bird must flap i.e. the region in which gliding is not possible. I have assumed that this region should be minimised if glide performance is at its optimum.

I carried out an experiment to investigate whether the elongated graduated tail of the magpie is a result of natural selection for increased glide performance. The effects of tail length elongation and reduction on magpie glide performance were measured. A diminution in glide performance with both tail elongation and reduction implies a naturally selected trait whilst a reduction in tail length leading to an increased glide performance implies sexual selection as an evolutionary mechanism (Evans and Thomas 1997).

MATERIALS AND METHODS

Magpie (*Pica pica*) chicks were removed from nests in the Stirling area in May 2000 (Scottish Natural Heritage, Bird scientific license: 1939). Two chicks were removed from each of five nests when between 15 and 25 days old (n=10).

Hand-rearing

Chicks were hand-reared on a combination of Low energy hand-rearing formula (The Birdcare Company, Vetafarm Europe Ltd.UK), boiled chicken eggs, beef mince, chicken mince and mealworms (see(Whitmore and Marzluff 1998)). Initially chicks were fed every 2 hours from 7am to 7pm. Time between feeds was gradually increased until birds were capable of feeding themselves. Initially chicks were kept indoors in open boxes and subsequently indoors in small cages. Hand feeding was continued until birds would no longer accept food from the hand. At 35 days old (16 days after removal from wild) all chicks could feed themselves. Two weeks after initial removal from nests, chicks were transferred to an outside aviary. Birds were then fed on dog food (a combination of dog meat and dried biscuits soaked in water), fruit, raw chicken eggs and fresh raw meat (see Plate 2.).

Flight training

Two perches were constructed at either end of a flight cage 8.5 metres long, to allow the birds to fly the full length of the cage. Gliding flight was encouraged by putting one perch at 2 metres above the ground and the other at 50 cm above the ground at either end of the cage. The cage wall behind the lower perch was covered in polythene sheeting to encourage birds to land only on the perch. Food was placed near to the lower perch in a feeding tray on the ground to encourage this behaviour.

Biometric measurements

Biometric measurements of each bird were taken, these were left and right wing

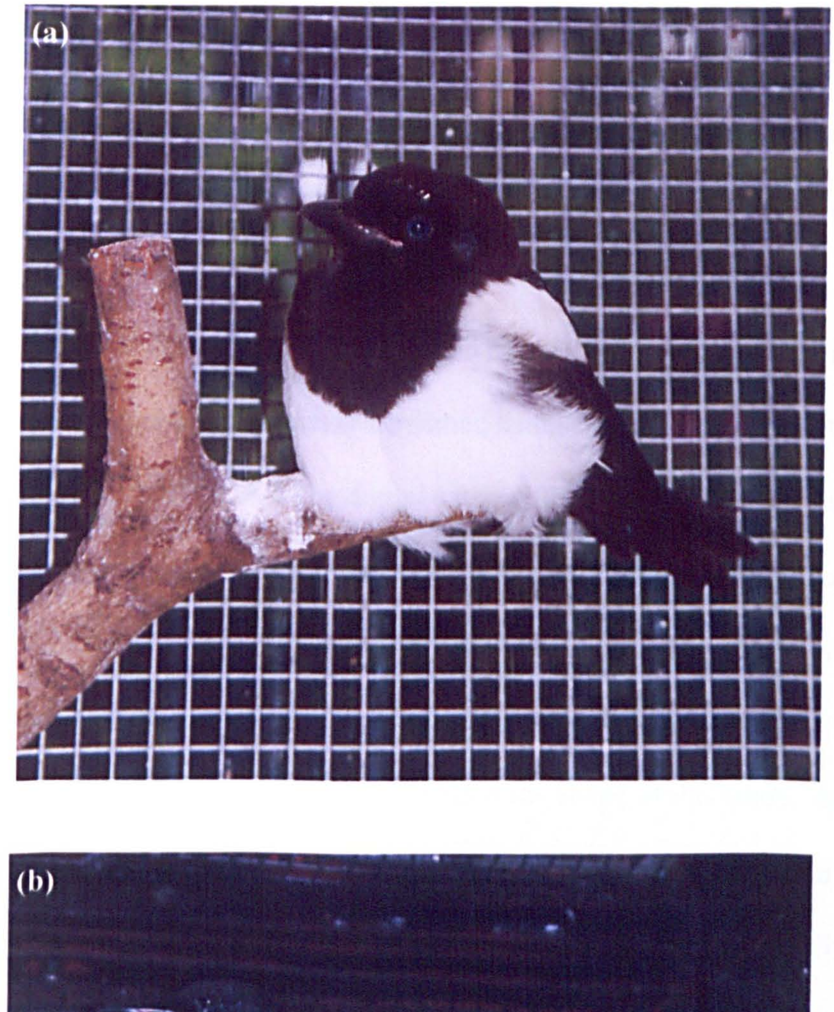


PLATE 2. Black billed magpie (*Pica pica)*
hand reared in captivity for flight experiments (a) 30 days old and (b) 8 months old

length (maximum wing chord); and length of six central tail feathers measured to nearest millimetre with a ruler; right and left tarsus to nearest 0.1 millimetre with callipers; body mass was measured to nearest 5g using a pesola spring balance. Paired measurements were averaged to calculate mean wing and tarsus length.

Data collection

Data collection commenced when all birds had completed their post-fledging moult and become proficient flyers. Birds were filmed using a camera placed at the lower perch end of the flight cage. A Sony digital camera (Sony Digital Handycam DCR-VX1000E) was used to film birds repeatedly gliding from the high perch down to the food tray. Within the confines of the cage all birds consistently flew in a straight line from high perch to feed tray. Whether this constraint on flight path had any influence on bird flight could not be tested within the scope of this study. However, all birds were tested within the same environment and each bird was treated as its own control, all birds were tested with at least three different tail lengths. This uniformity of flight direction and character allowed calibration graphs to be created to measure the distance of the bird from the camera and its height above the ground through-out each flight.

Distance from camera:

Each individual bird was filmed at a series of known distances from the camera. The video was digitised using the miro-MOTION DC20 digitiser (Pinnacle systems, UK). The video footage was then edited to select the frames of interest using Adobe Premier 4.2 on an Apple Macintosh 9500. The width of the bird's white breast patch was measured in pixels for each distance from the camera using NIH Image (available on the Internet at http://rsb.info.nih.gov/nih-image). Each bird was filmed three times and the width averaged. The equation of the relationship between bird width and distance from camera was found by fitting a power curve in S-plus 4.5 to the data for each bird (figure 1). The relationship in all cases approximated to an inverse relationship as indicated in figure 1. There was no significant difference found between birds (t=1.88, p=0.11, n=6). This relationship was then used to calculate the bird's distance from the camera when in flight.

Height above ground:

A metre ruler was filmed at known distances from the camera to allow a calibration graph of height at known distances to be calculated, method as above. This allowed the number of pixels per metre, at known distances to be calculated and allowed the height the bird descended during gliding flight to be found, once its distance from the camera was known.

For each gliding flight of an individual magpie the velocity and angle of descent (here after glide angle) could then be calculated. In order to film the birds in undisturbed gliding flight the video camera was set up and left unattended. A total of 145 hours of video footage was collected from the beginning of December 2000 to the end of March 2001.

Glide angle - angle of descent calculated from height dropped over distance travelled.

Velocity - Calculated from the time (frames-25/sec) taken to travel the distance from start to finish, distance travelled taken to be the hypotenuse distance rather than the horizontal distance travelled.

Gliding ability

The basis of glide performance calculations is the relationship between a bird's sinking speed and its forward speed. This is a curved relationship called a glide polar (Pennycuick 1989).

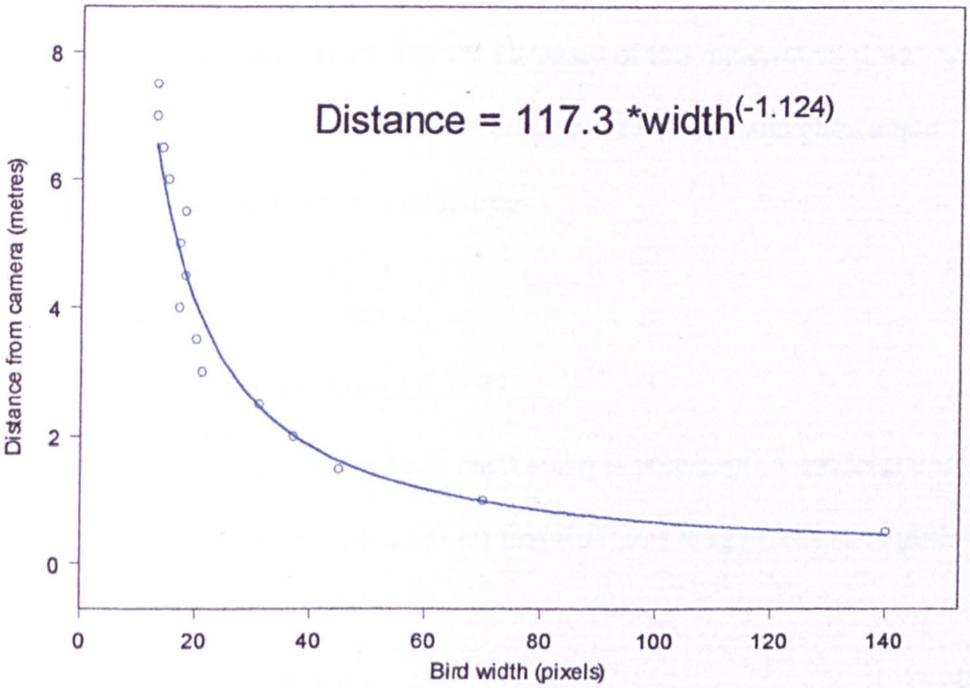


Figure 1 . Relationship between bird width and distance from camera for one individual.

A bird's sinking speed can be calculated from:

$$V_s = V\sin\theta \tag{1}$$

(McGahan 1973)

where V_s is sinking speed, θ angle of descent and V is forward velocity.

The bird's sinking speed is thus dependent on the bird's angle of descent and forward velocity. Equation (1) describes the relationship between sinking speed, forward speed and glide angle. For the purposes of this experiment it was necessary to consider only the relationship between forward velocity and glide angle.

Sinking speed is also related to total drag:

$$V_s = \frac{DV}{mg} \tag{2}$$

(Pennycuick 1989)

where D is total drag, m is the body mass and g is acceleration due to gravity.

By combining equations (1) and (2) we find that total drag is related to glide angle by:

$$V\sin\theta = \frac{DV}{mg} \tag{3}$$

Velocity on each side of the equation cancel out and the weight of the bird can be removed as each calculation is on the same bird and thus assumed to remain constant giving:

$$\text{Sin}\theta = \text{Drag x constant} \tag{4}$$

Drag is divided into three components, Parasite drag ($D_{par,}$) Profile drag (D_{pro}) and Induced drag (D_{ind}) which all depend on a bird's velocity. The three drag components are related as follows:

$$\text{Drag} = D_{par} + D_{pro} + D_{ind} \tag{5}$$

$$\text{Drag} = \frac{V^2SCd}{2} + \frac{V^2Ae}{2} + \frac{K}{V^2} \qquad (6)$$

(Pennycuick 1989)

Where Cd is the drag coefficient, S is body frontal area, K is a dimensionless 'induced drag factor' and Ae is wing area.

Following simplification of the equation, due to all flights being from the same individual, the relationship between velocity and glide angle for an individual bird can be described as:

$$\sin\theta = K_1V^{3/2} + K_2'V^2 + K_3V^{-2} \qquad (7)$$

$K_1 - K_3$ are all individual bird specific constants.

As stated earlier, the conventional means of measuring a bird's glide performance is to calculate a glide polar relating a bird's forward speed to its sinking speed. As shown in equation (1) a bird's sink speed is related to velocity and angle of descent. Glide angle and sink speed can be taken to measure the same basic component of gliding flight, a measure of the downward component of the glide. The conventional method of using forward velocity in the calculation of a bird's sinking speed means that forward velocity and sinking speed are intrinsically related to each other. In this work the relationship between a bird's angle of descent and forward speed was used as an alternative representation of a glide polar. Glide angle was calculated from distance travelled and distance dropped, whilst velocity was calculated as time taken to travel a given distance, as such these were considered to represent two independent measures of bird flight.

The relationship between gliding angle and velocity was used to investigate effect of changing tail length on magpies' glide performance. This relationship predicts that below a certain velocity and glide angle birds can no longer glide and must resort to flapping flight. The position of the function relating glide angle to velocity provided a quantitative measure of an individual's gliding ability. The area under the curve represents the region in which the bird must resort to flapping flight to remain air borne (figure 2). The position of the curve representing the lower limit of glide capability and the area cut off by it was then used to investigate the effects of changing tail length on an individual bird's gliding ability.

Finding the position of the curve relating glide angle to velocity

Fifteen flight paths of gliding flight were videoed for each bird with a given tail length. Each bird was individually colour marked (Pantone Inks, Letraset) on its white breast to allow easy identification of different birds. The flights were analysed as described above to find velocity and glide angle. The velocity and glide angle of each flight was then plotted. The lowest six positions of the fifteen were used to define the initial position of the curve describing the lower limit of the relationship between glide angle and velocity. The lowest six points were found by drawing a line between six points so that all other data points were to the right of the line. A non-linear regression was carried out in S-plus (2000) applying equation (7) to the six lowest data points. An equation for the line was then produced from the coefficients of the regression and the position of the curve found. Note that this method relies on the relationship between glide angle and velocity, and estimates the individual specific constants K_1-K_3. Further video of gliding flight was then collected. The final position of the curve was taken to be when the addition of five more data points of velocity versus glide angle had no effect on the position of the curve i.e. all values were above the lower bound of the relationship between velocity and glide angle (figure 3). Once the position of the curve was determined,

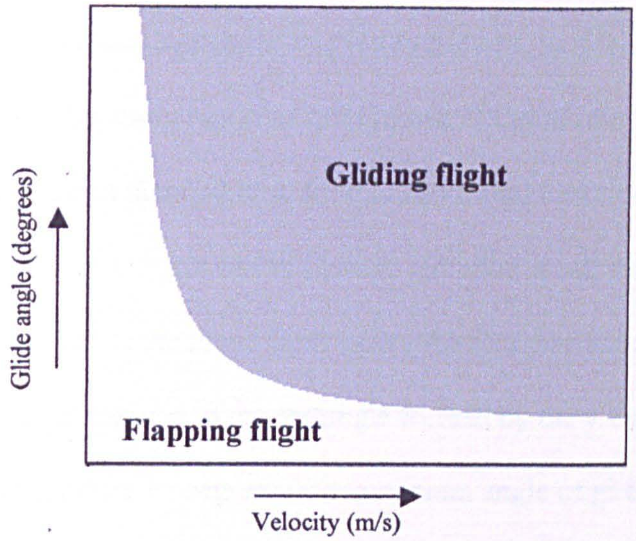
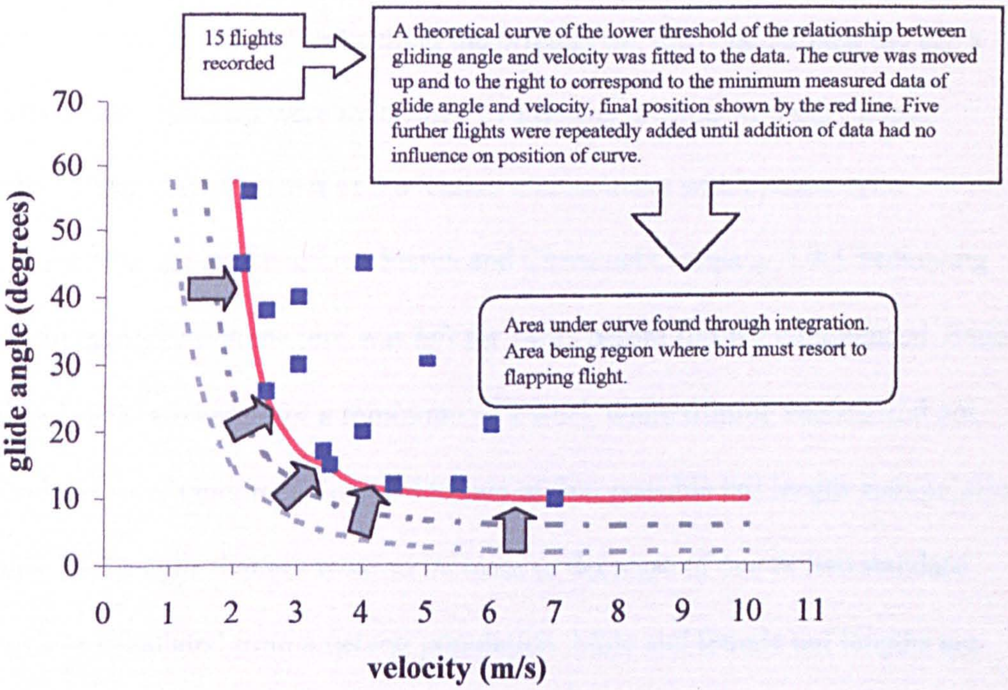


Figure 2. Theoretical relationship between velocity and glide angle.


15 flights recorded

A theoretical curve of the lower threshold of the relationship between gliding angle and velocity was fitted to the data. The curve was moved up and to the right to correspond to the minimum measured data of glide angle and velocity, final position shown by the red line. Five further flights were repeatedly added until addition of data had no influence on position of curve.

Area under curve found through integration. Area being region where bird must resort to flapping flight.

Figure 3. Finding the minimum glide angle and velocity below which an individual bird must engage flapping flight.

the area under the curve was calculated by integration. The upper velocity was limited to 15m/s above which the angle was difficult to discriminate from zero. The lower limit was set using two different criteria. Either as the lowest velocity recorded during that manipulation for that individual bird (lowest glide speed) or arbitrarily as 1.5 m/s which was the lowest recorded speed over all flights measured. The area to the left of the lower limit where the bird was not recorded as gliding was calculated as the area of the rectangle formed by the y axis and the lower limit velocity multiplied by 90 degrees (the maximum angle of glide possible). This area was then added to the area under the curve calculated through integration to give the total area in which gliding flight cannot occur.

Tail manipulations

Manipulations were carried out on the central six feathers of the bird's tail. Tail manipulation was achieved by removing the feather tip, removing or adding the required length of tail and reattaching the original tip, thus maintaining the tail's natural shape. Feathers were reattached by inserting a 5mm wire pin (0.6mm gauge, <10mg) into the shaft of the feather and securing with cyanoacrylic superglue (Permabond, National Starch and Chemical Company, UK). Following each tail manipulation the bird was left for 24hrs before filming commenced. Each bird had each tail length for a minimum of 1 week while filming was carried out. Individuals were randomly allocated to two of four possible tail length manipulation groups. Tail length changes were an increase or decrease of one or two standard deviations calculated from a natural population. Male and female tail lengths are significantly different but the length of one standard deviation is reported to be the same for both sexes (1 s.d. = 10mm (Cramp and Perrins 1994)). Where possible each individual was also subject to two control groups. Control 1 was an unmanipulated natural tail; control 2 was a tail of the naturally observed tail length subject to the manipulation technique as described above. Birds without a full, undamaged tail could not be subject to control 1 (n=3). In these cases the tail was re-constructed to an average tail length (calculated from the three birds with a complete natural tail) using the same method of feather attachment as described with complete feathers from other birds (control 2).

Statistical analysis

Due to the presence of repeated measurements on individual birds in the experimental design Residual Maximum Likelihood (REML) was used to analyse the data (Genstat release 4.1).

Area under curve (variable lower limit)

An analysis was undertaken to look at the effects of various fixed effects on the area under the curve. The fixed effects were manipulation size, manipulation size^2 (covariates) and manipulation technique (whether tail cut or not). The effects of weight, tarsus length and wing length (covariates) were also tested. Individual bird was included in the model as a random effect. REML can produce estimates of the amount of variability due to random effects such as individual bird (Horgan and Hunter 1993). Manipulation technique was constrained within the model regardless of its significance. The residuals of the data were checked for normal distribution and homoscedasticity. The significance of the terms was determined using the Wald statistic which is a chi-square distribution.

Lowest Velocity

The use of the lowest recorded glide velocity to fix the lower limit for the integration calculation meant that any effect of manipulation on lowest recorded velocity would inevitably be included in the subsequent analysis. A problem with this method was that any effects on lowest recorded velocity and on changes in the function relating glide angle to velocity could not be distinguished. Variation in lowest recorded velocity could lead to differences in calculated area under the curve even if the curve remains in the same position. An analysis of the effects of manipulation size, manipulation size ^{2}, wing length and manipulation technique on lowest velocity was carried out. Individual was included in the model as a random effect, manipulation technique was retained in the model regardless of significance.

Area under curve (fixed lower limit)

The area under the curve was recalculated with an arbitrary lower limit for the integration calculation of 1.5m/s (the lowest recorded velocity from all bird flights). This removed any effects of lowest velocity on the area under the curve and considered only movements in the position of the curve. The analysis was carried out in the same way as that for area under the curve using lowest velocity as the lower integration limit.

The minimum point of the curvilinear relationship between area and manipulation size was found by differentiation. The minimum point on a curve, the manipulation size at which the rate of change of the function becomes zero can be defined as df/dx=0. Bootstrapping was used in S-plus 4.5 to generate a population of minimum points from the original data set. This allowed 95% confidence intervals for the turning point to be calculated.

RESULTS

The area in which individual magpies could no longer sustain gliding flight was found to increase when the tail was either reduced below the naturally observed tail length or extended beyond it. The final data set included data from six different magpies. Of the original ten chicks, three died and one was excluded due to severe tail damage.

Area under the curve (variable lower limit)

The lowest glide speed recorded for the individual during that manipulation was used as the lower threshold for the integration calculation of the area under the curve. The most significant factor determining the area under the curve was found to be manipulation size^2, this describes a quadratic function or a U-shaped curve (table 1). The only other factor found to have a significant effect on area was wing length. As wing length increased, glide performance was found to increase; the area under the curve was reduced. There was no significant effect of manipulation technique, manipulation size, weight, tarsus or individual bird.

Lowest glide speed.

The lowest glide speed was significantly affected by manipulation size^2 (table 2). Increasing and decreasing tail length leading to an increase in the lowest glide speed observed again indicating a U-shaped curve. Of the other variables tested only wing length was found to significantly influence lowest glide speed. As in the previous analysis as wing length increased, glide performance was found to increase.

Area under the curve (fixed lower limit)

The area under the curve was recalculated with the lower limit set at 1.5 m/s. The most significant factor determining the area under the curve was again found to be manipulation size^2 (table 3). The results of the second analysis on area were the same as the first with the exception of the effect of wing length. In the second analysis this was no longer found to be a significant factor.

The coefficients from the REML analysis on area under the curve (variable lower limit) were used to calculate fitted values and standard errors for area over a range

factor	df	Chi sq	P
manipulation technique	1	1.05	0.307
manipulation size	1	0.74	0.389
wing length	1	6.55	**0.010**
manipulation size2	1	19.90	**0.000**

Table 1. REML statistical analysis for area (method 1: lower threshold of area calculation lowest glide speed)
(Fixed model: area = manipulation size+ manipulation size^2 + manipulation technique + wing length; Random model = individual)

factor	df	Chi sq	P
manipulation technique	1	3.66	0.056
manipulation size	1	0.11	0.745
wing length	1	4.63	**0.032**
manipulation size2	1	6.46	**0.011**

Table 2. Results of REML statistical analysis for lowest glide speed (Fixed model: lowest glide speed = manipulation size+ manipulation size^2 + manipulation technique + wing length; Random model = individual)

factor	df	Chi sq	P
manipulation technique	1	0.00	0.983
manipulation size	1	2.75	0.097
manipulation size2	1	4.09	**0.043**

Table 3. REML statistical analysis for area (method 2: lower threshold of area calculation arbitrary 1.5 m/s)
(Fixed model: area = manipulation size+ manipulation size^2 + manipulation technique + wing length; Random model = individual)

of tail lengths. The fitted values show the U-shaped curve described by the significant effect of manipulation size^2, increases and decreases of tail length away from the naturally observed length lead to an increase in the area under the curve. The threshold below which birds must resort to flapping flight shifts upward increasing the range of glide angles and speeds where the individual can no longer glide (figure 4).

A population of minimum points of the curvilinear relationship was generated through bootstrapping which allowed a turning point and 95% confidence intervals around the turning point to be calculated. The turning point was calculated as a median value of –0.00015mm with 95% confidence bands spanning zero (-0.0006 to 0.0016mm). In this instance zero represents the naturally observed tail length suggesting that the minima is not significantly different from zero.

DISCUSSION

The results suggest that the elongated, graduated tail of the magpie plays a role in determining the position of the curve describing the relationship between velocity and angle of descent during gliding flight. As such the results show that the length of the tail of the magpie influences its glide performance. This interpretation of the experiment relies on the assumption that the smaller the region in which a bird must resort to flapping flight the better. Gliding flight is a comparatively inexpensive form of flight (Rosen and Hedenstrom 2001) and is likely to be preferred to flapping flight wherever possible. Our results indicate that the naturally observed tail length of the magpie is optimal in terms of minimising the region in which a bird needs to flap. Deviations away from the naturally observed tail length lead to an increase in the size of the area where the bird must resort to flapping flight. This

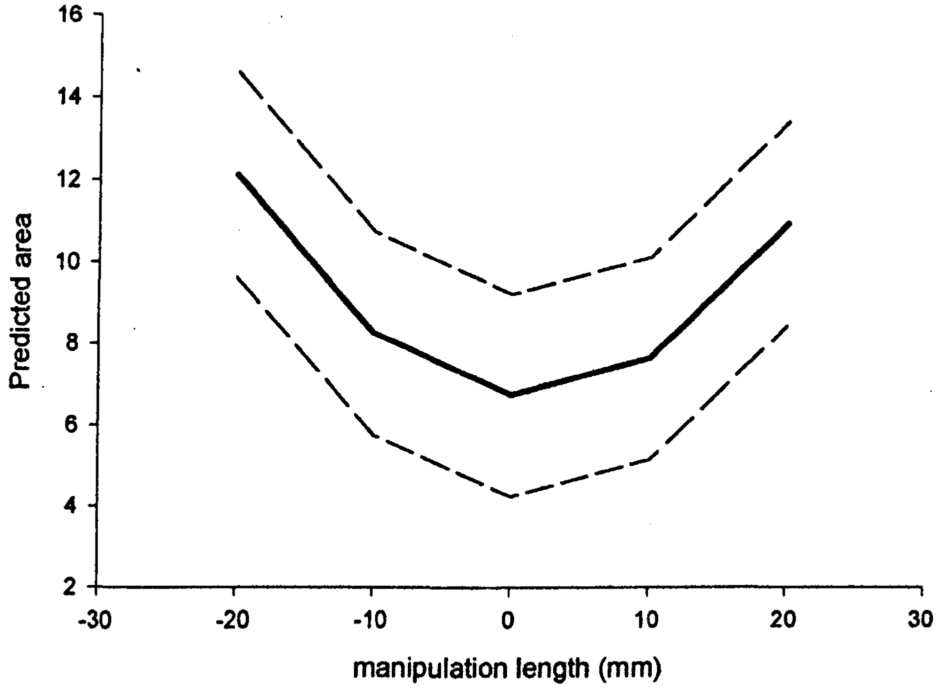


Figure 4. Predicted area (± 1 standard error) below threshold curve for different magpie tail lengths (calculated from REML coefficients, area method 1).

is indicated by the significant quadratic effect of manipulation. The confidence intervals of the turning point span zero suggesting that the optimal tail length for gliding is not significantly different from the naturally observed tail length. Lowest glide speed recorded for a bird also increases with changes in tail length. Birds with their natural tail were able to glide at slower speeds than birds with either elongated or reduced tail lengths. Increasing wing length led to an increased glide performance. Wing length influenced the lowest recorded glide speed and the area under the curve when lowest velocity was included within the area calculation. It was not found to have a significant influence on area when lowest glide speed was omitted. This suggests that the true effect of wing length was on lowest recorded glide speed and not on the shape of the function. There was no effect of manipulation technique observed during the experiment.

The results indicate that the magpies' elongated tail represents a naturally selected trait selected for its aerodynamic function. Whilst elongated graduated tails may not represent an optimum in terms of lift production, they can perform other vital aerodynamic roles. Many elongated tails of varying shapes may represent sexually selected ornaments. However, the possibility that such tails may perform a wide range of subtle aerodynamic roles must not be overlooked. It has been suggested that elongated graduated tails may passively stabilise a bird during flight. It is possible that increased stability provided by a graduated tail could increase the range of angles and velocities at which a bird could maintain gliding flight, lowering the position of the glide angle-velocity function.

Birds with different flight styles and ecology will be subject to varying selection pressures. This may have led to the evolution of a range of aerodynamic functions and associated tail shapes uniquely tailored to individual species requirements. For example, birds that live in cluttered environments may benefit from having a tail that's aerodynamic function is not substantially impaired by damage to outer tail feathers. Any damage to the outer feathers of a tail solely used for lift production severely reduces the tail's efficiency. Magpies are birds that generally inhabit open areas, they are ground feeders whose main food is invertebrates. It is a sedentary species with limited dispersal. As such flight could be said to play a relatively small role in the bird's life. Flight is not used during long migrations or during hunting for prey, two factors which may influence the evolution of a tail shape designed for lift production. In a bird such as the magpie, tail evolution may lead towards a tail designed to perform functions other than lift production. It may be that whilst the bird flies infrequently it reaps significant benefits from the flight it does undertake being as cost efficient as possible. This could be achieved by a lowering of the curve describing the relationship between velocity and glide angle, thus increasing the range of speeds and angles at which the bird can maintain gliding flight. The trade-offs between both ecological, behavioural and aerodynamic considerations represent an extremely complex issue but what is clear from this work is that the tail can play a vital aerodynamic role in terms of glide performance. In the magpie, the naturally observed tail length represents an optimum in terms of the range of glide angles and velocities over which an individual can maintain gliding flight.

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CHAPTER 4

Gliding flight, graduated tails and stability in birds.

INTRODUCTION

A bird's tail may play an important stabilising role during gliding flight (Hummel 1992). This would provide a mechanism through which tails could elongate aside from the conventional view of sexual selection leading to elongation. Studies of a Harris' hawk *(Parabuteo unicinctus)* in a wind tunnel indicate that the tail balances pitching moments produced by the wings thus stabilising the bird (Tucker 1992). It is possible that long tails may stabilise the bird passively in a similar way to the feathers on a dart (Alexander 1971; Evans and Thomas 1992). Recent work on the ring-necked pheasant (*Phasianus colchicus*) has shown that its elongated graduated tail is naturally selected to provide stability during gliding flight (Chapter 2). It was shown through the use of model birds that modifications of tail length away from the naturally observed length led to a decrease in a bird's stability. The naturally observed tail length represented the length needed for optimal stability.

Current aerodynamic theory suggests that the optimum tail shape of a bird's tail is one that is triangular when spread at 120° (Thomas 1993). Thomas (1993) suggested that an avian tail is analogous to a delta wing and applied slender lift surface theory to predict the forces generated by a bird's tail. He used this theory to make predictions about how the tail functions during flight. If the tail functioned as a delta wing, then the tail would continue to produce lift as long as the tail increased in width down its length. Any area behind the maximum continuous span would produce only drag (Lee and Ho 1990; Thomas 1993) thus reducing the overall lift produced by the tail. A graduated tail, where the central feathers are longest with a gradual reduction in feather length towards the edges of the tail, represents one such tail shape where tail area extends behind the tail's maximum continuous span. A role providing aerodynamic stability would provide a function for tail shapes other than triangular tails, shapes that are currently thought to be far from optimal for lift production such as graduated tails. It would provide a mechanism through which tail shapes other than triangular tails could have evolved via natural selection for an aerodynamic function. Such tail shapes are traditionally thought of as a product of sexual selection for a mate choice advantage, as in the elongated graduated tail of the ring-necked pheasant. If a graduated tail did increase stability during gliding flight, it could be hypothesised that there might be correlated evolution between the graduated tail shape and the occurrence of gliding flight. Birds with graduated tails would be more likely to adopt gliding flight.

Comparative analysis can be used to address questions about correlated evolution because different species can converge on the same adaptation through natural selection (Ridley 1983). One of the problems with a comparative approach is non-independence of data points. This arises because each species is part of a hierarchically structured phylogeny (Felsenstein 1985). Closely related species tend to be more similar than distantly related species and may exhibit similar traits (Pagel 1999a). There are two main reasons for this lack of independence, firstly it may occur because there has not been sufficient time for divergence to take place. Secondly, non-independence may arise because selection pressures are the same on two individuals that have similar phenotypic responses (Harvey and Pagel 1991). Each species is to a greater or lesser extent related to each other species. If phylogenetic associations of species are not taken into account, the data violates the statistical assumption of independence (Felsenstein 1985), which has the effect of inflating the degrees of freedom of the statistical test and the probability value cannot be trusted (Harvey and Pagel 1991). The issue of non-independence of data points in comparative analyses has been acknowledged for some time (Felsenstein

1985; Ridley 1983). Ridley (1983) and Maddison (1990) have proposed methods to overcome the problem of non-independence of data point when analysing discrete data. Ridley's (1983) method works by counting evolutionary events, where one or both traits change along a branch of the phylogeny. Where changes do not occur the branch is ignored (Pagel 1994). This method results in a 2x2 contingency table that is tested using the Chi-square (X^2) statistic (Harvey and Pagel 1991). Maddison's (1990) method looks at whether changes in one character are concentrated in a certain area of the phylogenetic tree. Both methods rely on one set of inferred character states at each internal node (Pagel 1994). Ancestral states are reconstructed through the use of parsimony, they choose the state which minimises the number of evolutionary events (Pagel 1999a). Pagel (1994) suggests that a more realistic approach to assigning a trait to an internal node would be a probability distribution of character states. This would look at the probability of each character state at each node and find those which were more parsimonious or probable (Pagel 1994). This is a maximum likelihood approach which works by using the observed data as a fixed observation and finding the statistical parameters that provide the most probable description of the data (Pagel 1999a). The maximum likelihood approach seeks the hypothesis that best describes the data (Pagel 1999b). However, it should be noted that the end result of any comparative analysis is influenced by inaccuracies in the phylogeny which cannot be known explicitly (Pagel 1997).

The objective of this study was to investigate the possibility of correlated evolution between gliding flight and the graduated tail shape which I hypothesised would result from a graduated tail playing a stabilising role during flight (Pagel 1997).

METHODS

A data set was compiled using the Birds of the Western Palearctic CD-ROM (Cramp 1998). Birds with graduated tails and birds with a gliding phase of flight were located. Information on a number of other features about the birds' structure and ecology were also collected. This information included total length of the bird measured from tip of bill to tip of tail; tail length measured from where the central tail feather emerges from the skin to the tip of the longest feather; whether any body structures were significantly sexually dimorphic either in colour or size; if the bird glided in any part of normal flight; if the bird migrated in any part of its range; whether flight was used during hunting; whether the bird lived in an open (grassland, sparsely wooded, water, reeds, wetland) or closed (wooded/dense bushes or scrub) habitat. Migration in birds is predicted to be indicative of long distance flight where lift production is likely to be more important than stability. In addition, it seems likely that birds that use flight during hunting will be subject to different evolutionary constraints than ground feeders. The habitat in which a bird lives is predicted to influence both tail shape and flight mode.

This allowed binary discrete characters for each species to be found, that is characters that can adopt only two states (Pagel 1999b). The traits considered were gliding flight, migration, sexual dimorphism and flight used to catch prey (aerial hunter), whether the bird possessed an elongated tail (defined as tail longer than body (Balmford *et al.* 1994)) and whether the bird lived in an open or closed habitat. Additional species of the same genus exhibiting neither a graduated tail or gliding flight were selected at random and added across all orders to give all four possible trait combinations in the data set (a total of 22 species). The searches carried out resulted in a sample of 114 species. The phylogeny associated with the 114 species was reconstructed with reference to Sibley and Ahlquist (1990) with additional information from Martin and Colbert (1996) and Cracraft (1981).

The data was analysed using a program called 'Discrete' (Pagel 1994). 'Discrete' is used to analyse binary characters on a phylogenetic tree. The program implements a continuous time Markov model in a maximum likelihood framework. The Markov approach looks at transitions among possible states of a discrete character and estimates rates of evolution between these possible states. These rates are then used to calculate the most probable ancestral states (Pagel 1997; 1999a). It allows the analysis of comparative data without the need to reconstruct ancestral states but rather sums the likelihood of all possible states. It tests for correlated evolution by testing the fit of two different models to the data. The first model assumes independent evolution, the second dependent or correlated evolution. It tests for a significant difference between the two models using the log-likelihood test statistic (LR), where LR= $-2\ln[H_o/H_1]$. It compares the fit of the independent model (H_o)(null hypothesis) with the fit of the dependent model (H_1)(alternative hypothesis). The test is asymptotically X^2 distributed with 4 d.f. if the two hypotheses are nested i.e. if the dependant model is a special case of the independent model (Pagel 1994). If the two hypotheses are not nested, the likelihood is not necessarily distributed as a X^2, in such a case the likelihood ratio statistic is used as a measure of support (Pagel 1999b). If H_1 is not a special case of H_o a Monte Carlo test procedure is required to obtain a p-value (Pagel 1994). A Monte Carlo procedure finds an approximate null hypothesis distribution from any likelihood ratio test (Pagel 1994) without making any assumptions about distribution. The Monte Carlo test in 'Discrete' uses the observed data to find the maximum likelihood set of parameters for a model of independence. The four maximum likelihood parameters derived from this are then fixed and used to evolve the two characters along the branches of the phylogenetic tree up to and including the tips (Pagel 1994). This null hypothesis of trait distribution is then tested against the independent and dependent models and likelihood ratios found. The simulation then produces a probability value of the likelihood of correlated evolution. The Monte Carlo test can thus be used to ascertain the level of significance of the test of correlated evolution (Pagel 1994).

'Discrete' requires a bifurcating hierarchical phylogeny, in order to meet these criteria the phylogeny of 114 species was simplified. Because of the need for a binary tree many species had to be removed from the analysis. Any polytomies in the tree (a node with more than two daughter branches) were resolved to bifurcations. Where closely related species had the same trait expression, e.g. both had graduated tail and gliding flight, the removal of one of these species would not remove the trait combination from the analysis and as such would not affect the analyses in any substantial way (Pagel, Discrete User Manual). Where it was not possible to satisfactorily resolve the tree to bifurcating branches species were removed randomly. This random removal lead to the number of species of the same genus in the final phylogenies being smaller than might be expected from the data collation method described earlier. As a result of this simplification two different phylogenies were tested, one including Passeriformes but not Ciconiiformes or Gruiformes, comprising 26 species with 24 internal nodes (figure 1) and a second including Ciconiiformes and Gruiformes but not Passeriformes, comprising 25 species with 23 internal nodes (figure 2). Due to the different sources used to compile the species phylogenies, all branch lengths were assumed to be equal. This implies a punctuational view of evolution (Pagel 1994) but Cezilly et al. (2000)

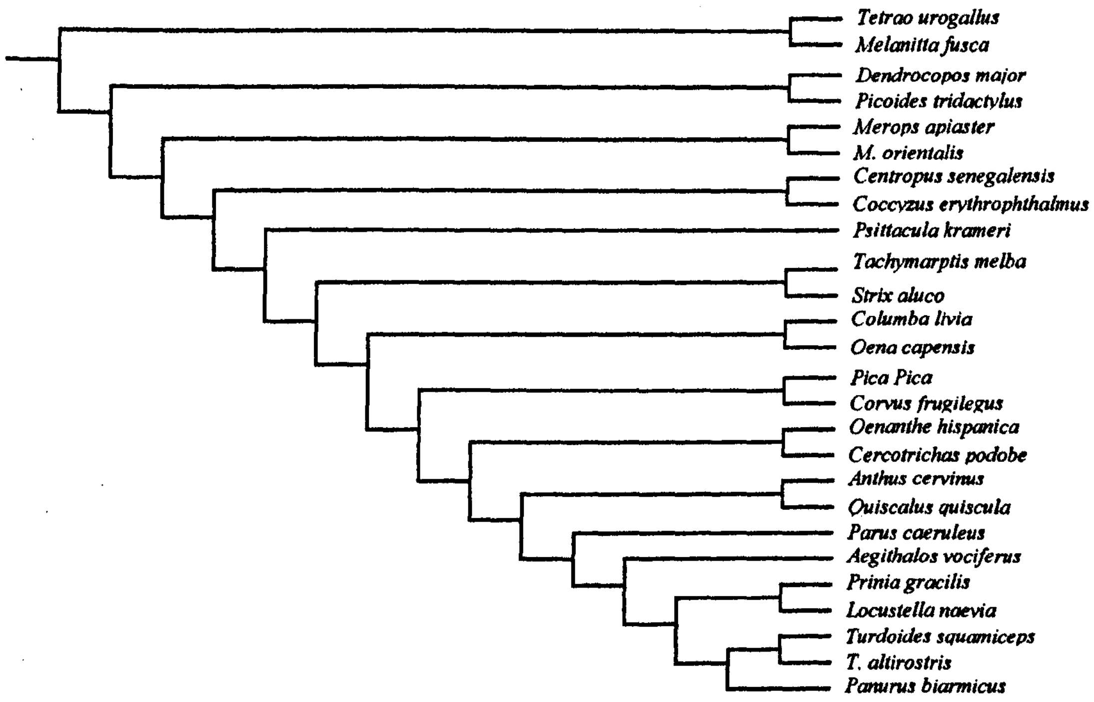

Figure 1. Bifurcating phylogeny including Passeriformes.

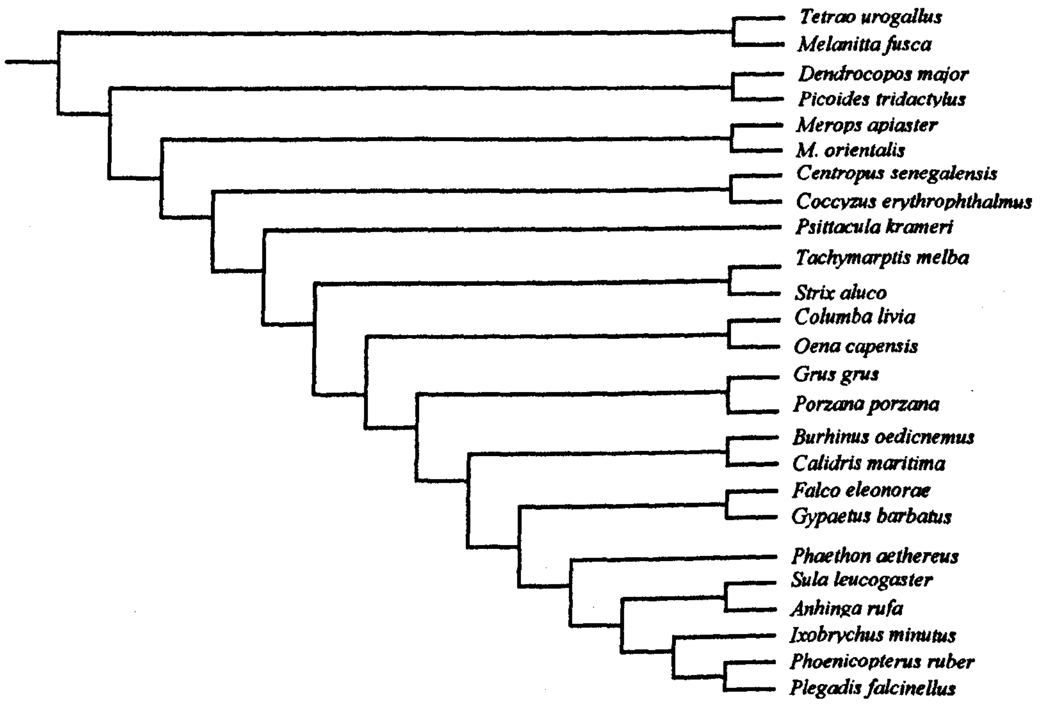

Figure 2. Bifurcating phylogeny including Ciconiiformes and Gruiformes.

suggest that assuming equal branch length does not affect the results quantitatively. 'Discrete' was used to test for correlated evolution between gliding flight and graduated tails in birds for both phylogenies. The null hypothesis (H_o) was of independent evolution and the alternative hypothesis (H_1) of correlated evolution. H_1 is best thought of as not being a special case of H_o (M.Pagel, personal communication) and a Monte Carlo simulation was applied. In all cases the simulation was run 100 times. Following the test for correlated evolution between gliding flight and a graduated tail both gliding flight and graduated tail were tested separately for correlated evolution with each of the morphology and ecology variables in the data set.

RESULTS

Gliding flight and graduated tails.

The results of the test for correlated evolution using 'Discrete' (Pagel 1994) indicate no correlated evolution between the use of gliding flight and graduated tails in birds. This was the case for both the phylogeny that included Passeriformes and that which included Ciconiiformes.

Phylogeny including Passeriformes.

The log-likelihood of the model assuming independent evolution of the two traits was –34.27, compared to the dependent log-likelihood of –32.74. This represents a log-likelihood ratio of 3.05 (df=4, ns). A Monte Carlo simulation was carried out to remove the asymptotic assumption. After 100 simulations the probability of such a difference occurring under H_0 was found to be 0.23.

Phylogeny including Ciconiiformes and Gruiformes

The log-likelihood of the model assuming independent evolution of the two traits was –32.1, compared to the dependent log-likelihood of –31.7. This represents a log-likelihood ratio of 0.76 (df=4, ns). The Monte Carlo simulation gave a probability value of 0.72.

Other ecological and morphological traits.

Following the tests for correlated evolution between gliding flight and a graduated tail other morphological and ecological factors were tested for correlated evolution. Each test was carried out on both phylogenies.

Correlated evolution with gliding flight.

For both phylogenies migration, habitat type, aerial hunting, sexual dimorphism and elongated tail were tested for correlated evolution with gliding flight. It was found that none of the morphological or ecological traits were correlated with gliding in flight when a Monte Carlo simulation was applied (table 1).

Correlated evolution with graduated tail.

For both phylogenies migration, habitat type and sexual dimorphism were found to evolve independently of graduated tails (table 2). The phylogeny including Ciconiiformes was found to have significant correlated evolution between the graduated tail trait and tail elongation. The Passeriformes phylogeny was similarly found to show correlated evolution between graduated tail and tail elongation and also for graduated tail and a lack of the use of gliding flight whilst hunting for food (table 2). The dependent evolution model produces a matrix of transition probabilities for the transition of each trait combination. This matrix allows specific comparative hypothesis to be considered (Pagel 1994). The nature of the correlated evolution can thus be considered in more detail. A flow diagram of the transition

Trait correlated with gliding	**L(I)**	**L(D)**	**LRS**
Phylogeny including Ciconiiformes and Gruiformes			
Migration	-32.26	-31.80	0.94
Habitat	-26.97	-26.62	0.70
Sexual dimorphism	-31.25	-30.85	0.82
Elongated tail	-23.88	-23.84	0.08
Aerial hunting	-29.55	-26.77	5.56
Phylogeny including Passeriformes			
Migration	-34.58	-33.94	1.28
Habitat	-33.00	-31.85	2.32
Sexual dimorphism	-32.39	-30.85	3.08
Elongated tail	-33.28	-32.37	1.82
Aerial hunting	-25.40	-24.78	1.24

Table 1. Correlated evolution of gliding flight with ecological and morphological traits. (L(I) independent likelihood, L(D) dependent likelihood, LRS likelihood ratio statistic, $p<0.05$*, $p<0.01$**, $p<0.005$***)

Trait correlated with a graduated tail	**L(I)**	**L(D)**	**LRS**
Phylogeny including Ciconiiformes and Gruiformes			
Migration	-32.59	-30.24	4.68
Habitat	-27.30	-26.51	1.58
Sexual dimorphism	-31.58	-29.23	4.70
Elongated tail	-24.21	-20.73	**6.98***
Aerial hunting	-29.87	-29.35	1.04
Phylogeny including Passeriformes			
Migration	-34.58	-33.32	2.52
Habitat	-33.01	-31.96	2.10
Sexual dimorphism	-32.39	-32.23	1.32
Elongated tail	-33.29	-25.69	**15.2*****
Aerial hunting	-25.41	-21.47	**2.86***

Table 2. Correlated evolution of graduated tail with ecological and morphological traits. (L(I) independent likelihood, L(D) dependent likelihood, LRS likelihood ratio statistic, $p<0.05$*, $p<0.01$**, $p<0.005$***)

rates can be produced to describe correlated evolution between graduated tails and tail elongation (Figure 3). The transition probabilities of the dependent model indicate that the most probable transitions are from 0,1 to 0,0 and from 0,1 to 1,1. That is from a non-graduated but elongated tail to either a tail which is both graduated and elongated or a tail which is neither graduated nor elongated. Restricting the transition probabilities of these two transitions to zero can test this more formally. The restricted model is compared to the full, unrestricted model through the maximum likelihood statistic. If the unrestricted model fits the data better than the restricted model then the restricted transitions are significantly different from zero (Pagel 1994). It was found that the unrestricted model described the data significantly better than the restricted model (LRS=27.8, $p<0.005$, 2d.f.). None of the other transition parameters were found to be significantly different from zero. Both phylogenies gave the same results in the transition parameter matrix. The transition matrix for correlated evolution between graduated tails and aerial hunting in Passeriformes indicates that the highest transition is away from aerial hunting when a bird has a graduated tail. Comparisons of transition parameters reveals that a bird is more likely to have a graduated tail if it does not hunt aerially and that evolution of aerial hunting is more likely if the tail is a shape other than graduated.

DISCUSSION

The results of this comparative analysis examining the relationship between tail graduation and gliding flight indicated that the evolution of graduated tails in birds is not correlated with gliding flight. However, following further investigation of other ecological and morphological factors correlated evolution was found between

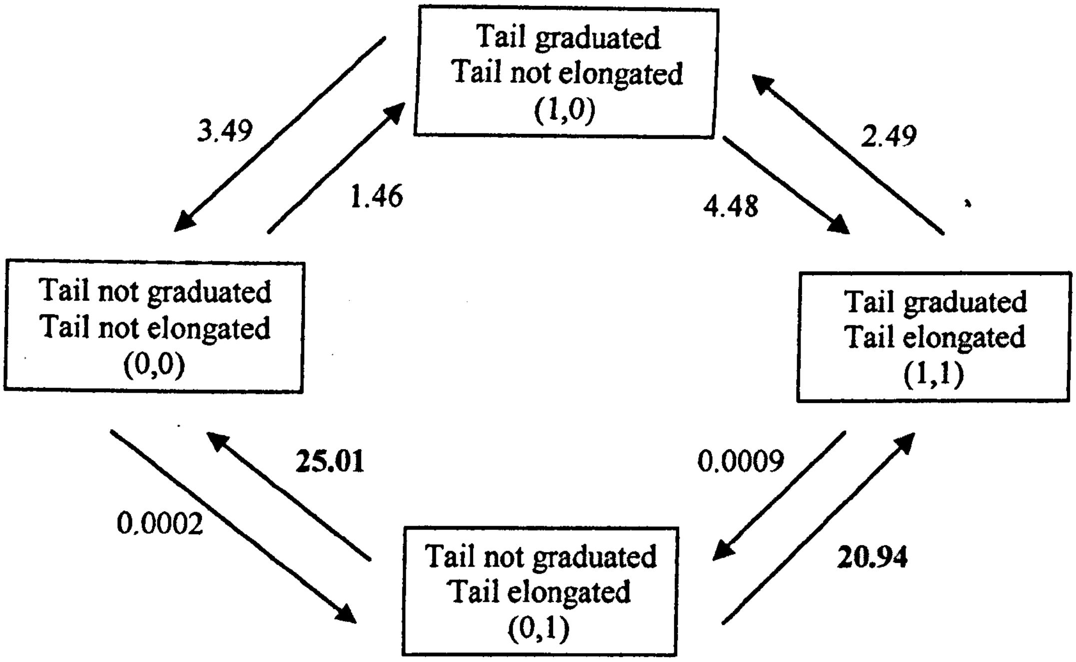

Figure 3. Transition parameter matrix of correlated evolution between graduated tails and tail elongation (Passeriformes phylogeny). (Numbers represent transition rate parameters, bold figures represent significant transitions)

graduated tails and elongation tails (tails were over 50% of a bird's total length). The aerodynamics of birds' tails represents a complex problem. Potentially the evolution of flight style and the shape of the tail can be influenced by ecological, morphological and behavioural factors. While it has been shown that in some species graduated tails provides stability during flight (ring-necked pheasant, Chapter 2) and increased glide performance (magpies, Chapter 3), the graduated tail may not always have an aerodynamic function. A potentially sexually selected role could be considered. It also seems probable that whilst a graduated tail could provide useful stability during gliding flight a bird may benefit from the tail providing some other function which would be best achieved from a considerably different tail shape. Within the data set tested here there were a number of factors that were not considered which may have a bearing on the results found. No measure of how often a bird takes flight was included or how often a bird glides during flight, these two factors would have an important impact on whether the selection pressures on a birds tail favoured an aerodynamic function over other factors. This test for correlated evolution between gliding flight and a graduated tail may represent too simplistic a view of the two traits. The data needed to eliminate these potential influences on correlated evolution would include behavioural observation fieldwork to obtain data on time spent gliding and the proportion of time spent gliding whilst in flight. Data would need to be obtained for a range of different species. This data collection was beyond the scope of this study but would represent an interesting direction of future work.

The correlated evolution found between graduated tails and tail elongation may provide indirect evidence of the graduated tail playing a role in stability. The dependent model matrix indicated that the most probable transitions were from a non-graduated but elongated tail to either no elongation and no graduation or elongated and graduated. Graduated tails are significantly more likely to be elongated than non-elongated. This suggests that the graduated tail represents a secondary trait, it evolves from a pre-existing long tail. Hummel (1992) suggests that long tails are a means to increase stability. He showed that stability increases linearly with tail length and that the size and planform shape of the tail control the stability of a bird. One would think that it would be counterproductive for a bird to evolve an elongated tail to increase stability if the tail shape did not evolve to enhance this function. It might therefore be implied that whilst correlated evolution was not found between gliding flight and graduated tails for increased stability, the correlated evolution of graduated tail and tail elongation may hint at a link between graduated tails and stability since elongated tails have been shown to increase stability and are shown to have significant correlated evolution with graduated tails. It is possible that birds that use flight as an important part of hunting would benefit more from a tail that produced lift rather than one that aided stability. As such you might expect birds that fly frequently to have a tail shape nearer to triangular, optimum for lift production rather than other tail shapes. This would explain why aerial hunters tend to evolve tails that are not graduated.

An alternative would be to explain the observed pattern of evolutionary change in terms of sexual selection. An elongated non-graduated tail could represent a sexually selected trait. If the tail was elongated through sexual selection recent evidence suggests that the trait could either increase in elaboration, for example become graduated, or alternatively be lost altogether (Wiens 2001). Much past work has concentrated solely on the ideas of traits becoming further elaborated through female preference. However, recent work suggests that traits and/or female preference can equally frequently be lost. Factors implicated in the process of trait loss include environmental factors such as increased predation risk due to the presence of the ornament and nutritional costs of trait maintenance, random factors such as genetic drift and social factors. The traditional view of unidirectional sexual selection may be incorrect with trait loss in males being common (for review see Wiens 2001)). The results found here indicated that two possible transitions are most likely, elongated non-graduated tails either become graduated or lose the elongation. If the tail was sexually selected as a mate choice ornament the tail may become further elaborated by becoming graduated. Alternatively the elongated trait may be lost as described by the transition from elongated, non-graduated tail to neither elongated or graduated tail.

The data presented here indicates correlated evolution between tail elongation and the graduated tail shaped. However, the exact evolutionary mechanism (natural or sexual selection) can only be speculated upon. Evidence presented in chapters 2 and 3 indicate a naturally selected function for the elongated graduated tail rather than a sexually selected one. Whilst the results of this comparative analysis do not provide direct evidence of natural selection for an aerodynamic function they do not rule it out.

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CHAPTER 5

The aerodynamic role of the avian tail during gliding flight.

INTRODUCTION

The functions of the avian tail have been the centre of much discussion in recent years. One possible function is that the tail could act as a lift producing surface, engendering lift in addition to that created by the wings (Thomas 1996b). Such a tail could have an aerodynamic role during turning, slow and manoeuvring flight. An alternative function would be the tail acting as a control surface making minor compensatory movements during flight (Thomas 1993a).

The conventional theory for the aerodynamics of the avian tail was suggested by Thomas (1993a). The tail is considered to be a "thin flat delta-shaped wing of low aspect ratio". A delta wing can be thought of as being analogous to the shape of Concorde. In a standard aerofoil the air above the wing moves at a faster velocity than the air below the wing. Bernoulli's theorem describes steady flow along a streamline and states that where the velocity of a fluid is high, the pressure is low and vice versa (Alexander 1971). Air circulates around the edges of the wing from the high pressure below to the low pressure above. The shape of a delta wing is such that as the air moves around the edges of the wing two spiralling leading edge vortices are formed (Gad-el-hak and Ho 1985; Lee and Ho 1990) (figure 1). A substantial amount of the lift produced by the wing is thought to be a result of these vortices (Chang and Lei 1996; Kumar 1998; Luca *et al.* 1995). The result is a wing that produces lift and manoeuvrability well beyond the expectation of a standard aerofoil (Lowson and Riley 1995).

Thomas' (1993a) model of the aerodynamic properties of the tail and the forces acting on the tail was based on a modification of slender lifting surface theory and the tail functioning as a delta wing. The theory predicts that the lift produced by the tail is determined by its maximum continuous span, this is in contrast to the wings where lift produced is proportional to wing area (Thomas 1993a). As long as the tail is increasing in width down its length the tail continues to produce lift. Imagine a flat delta wing moving through a vertical plane at an angle of attack x. As the delta wing moves forward through the plane the circulation remains the same but the scale increases due to the increase in the span of the wing (figure 2). Mass is accelerated into the flow as a result of this increase in scale which results in lift production (Thomas 1993a). Lift production is limited by angle of attack, above a given angle vortices undergo a sudden expansion known as vortex breakdown and lift is lost (Lowson and Riley 1995).

Thus Thomas' (1993a) theory suggests that the tail produces lift and provides a mechanism for this lift production. However, the model makes a number of assumptions with regard to the tail being able to function successfully as a delta wing. The validity of some of these assumptions could be called into question.

(1) It is assumed that a bird's body in front of the tail doesn't affect its ability to function as a delta wing. It has been found that the apex geometry of a delta wing is the most important factor in determining when vortex breakdown leading to loss of lift occurs, apex shape being the most important parameter (Lowson and Riley 1995).

(2) It is assumed that the tail acts independently of the wings and that air flow over the tail is steady. Hummel (1992) states that the tail works in the downwash field of the wings and its effectiveness in terms of lift production is reduced as a result of this. Recent work suggests that interactions between the body and tail of the bird are critical in terms of the tail's aerodynamics,

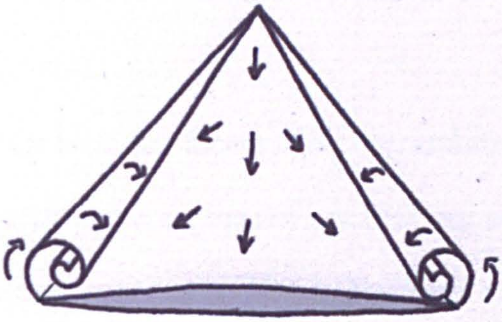


Figure 1. Air circulation over a delta wing.

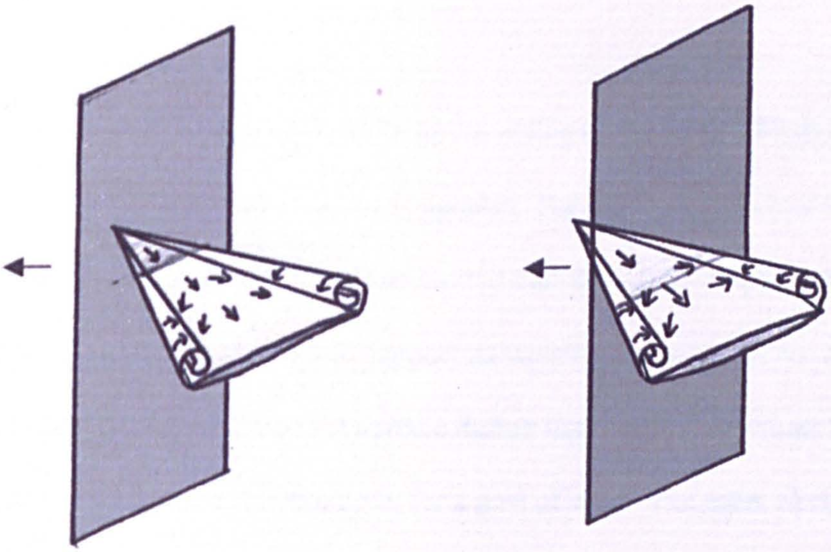


Figure 2. Lift production on a delta wing.

As the wing moves forward through a vertical plane the circulation about the wing remains the same but the scale increases. This increase in scale results in lift production and that vortices from the body interact with those of the tail, degrading tail lift (Maybury *et al.* 2001).

(3) The tail is assumed to be of low aspect ratio (long and slender). A tail spread at 120°, the predicted optimum tail spread for lift production (Thomas 1993a), has an aspect ratio of 7, which is high. A low aspect ratio wing would be a tail when furled. It has been found that the suggested optimal tail spread of 120° represents a tail that is beyond the spread at which a tail still functions as a delta wing, even at low angles of attack (Maybury *et al.* 2001). Maybury *et al.* (2001) concluded that the tail does generate lift but not to the same degree as the lift produced by an isolated delta wing.

Using Thomas' (1993a) model of the forces acting on a bird's tail two main functions for the avian tail could be suggested. The tail could produce lift in a way analogous to a delta wing. Thomas suggested that the tail could produce as much as 1/3 of the total lift a bird needs to support its weight (Thomas 1993b). Alternatively, the tail may function as a control surface during flight, tail movements being initiated to compensate, for example, for a gust of wind. The most likely mechanism for providing this control would be lift production. In this case, as the lift is a correction factor, the length of time that lift was produced in any give direction would be much less than that produced if a tail contributed an important element of lift. Predictions about tail morphology and movement during flight can be used to distinguish between these hypotheses about tail function.

This study used stereo-video techniques to gain detailed descriptions of bird tail movements during gliding free flight. Predictions associated with each of the two alternative hypothesis of tail function were made and tested using the data on bird movement. Harris' hawks (*Parabuteo unicinctus*) (Plate 3) were used as a study species due to their large size enabling detailed positional data to be measured and their slow gliding flight which enabled 25Hz video cameras to be used to obtain data.

MATERIALS AND METHODS

Data collection

Seven Harris' hawks (*Parabuteo unicinctus*) from a number of different falconry centres in different geographical parts of the UK were used during the study over a period from July 1999 to May 2001. The Harris' hawks were all trained to fly to a leather glove and were handled by their regular falconer. All birds were controlled with the use of jesses and food rewards. They were filmed in free gliding flight from either a perch or tree to a falconer's glove over the top of the cameras. These short flights encouraged the bird to glide at slow speeds with an unfurled tail. The flight was standardised as much as possible to allow direct comparisons between different flights of individuals and different individuals. Filming was carried out using two Sony cameras (Sony Digital Handycam DCR-VX1000E) mounted on a rigid bar 1 metre apart (Plate 4). The cameras were synchronised at the start of filming to gain stereo-video footage of the bird in flight. The cameras were held level and mounted at 90° to the horizontal bar, a standard object of known size was filmed at the start of each filming session to check the error associated with the set-up. The error associated with the standard object length was 4 % (se± 0.7%, n=40). Buchanan and Evans (2000) calculated estimated error on the same set-up to

PLATE 3. (a) Harris' hawk (*Parabuteo unicinctus)*

PLATE 3. (b) Harris' hawk (*Parabuteo unicinctus)* coming into land highlighting triangular tail shape

PLATE 4. Harris' hawk (*Parabuteo unicinctus)* sitting on stereo video camera set up used to collect data on body movements during flight.

be 6.1% (se± 2%, n=92). They found the error of positional data for distance from cameras and position in the field of view to be <10%. Error associated with measures of velocity has been estimated at 10.2% (se± 3.2%, n=6) (Evans, Buchanan and Park unpublished data).

Flight calculations

The stereo-video technique allowed a three-dimensional flight path of the bird to be reconstructed. The stereo-video was digitised using the miro-MOTION DC20 digitiser (Pinnacle systems, UK) on an Apple Macintosh 9500. The position of the bird in each frame of flight (frame rate was 25 frames/s) could then be calculated. The digitised footage was edited using Adobe Premier 4.2. The public domain NIH-image program (available at http://rsb.info.nih.gov/nih-image/) was used to obtain 2-D co-ordinates for various positions on the bird's body for each frame. Positions were obtained for the wing tips, the bird's head, the tail apex and both tail tips (figure 3). The co-ordinates of these positions on the bird's body were obtained for both the left and right cameras. The 3-D co-ordinates related to these positions on the bird in flight was calculated using the focal length of the cameras, camera separation and the stereo pairs of 2-D co-ordinates. The 3-D co-ordinates were smoothed using a fourth-difference algorithm (Rayner and Aldridge 1985). The smoothed co-ordinates were then used to calculate various aspects of the bird's movements during flight in three-dimensional space (figure 4).

Tail spread was calculated from the left and right tail tip and tail apex positions. Tail width and the length of the sides of the tail were used to calculate the angle of spread at the tail apex.

Tail bank angle from the horizontal was calculated from the position of the left and right tail tips (y co-ordinate only) and the tail width.

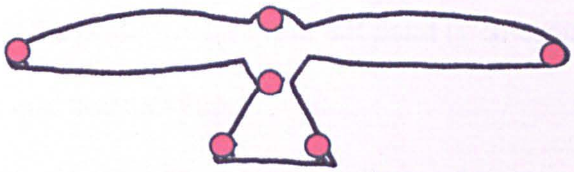
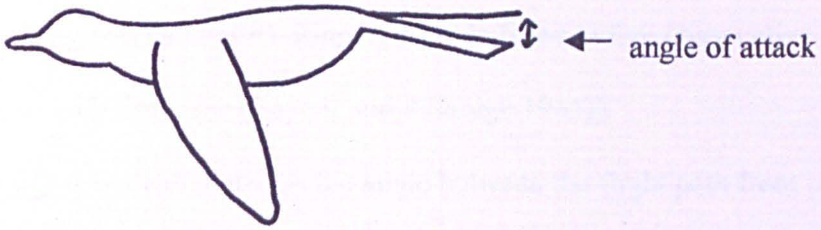
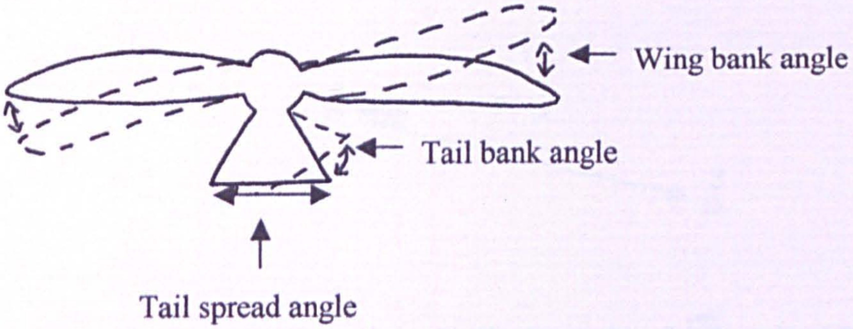


Figure 3. Positions on bird recorded from video footage. Red dots indicate co-ordinated recorded



a) Angle of attack



b) Tail spread, wing and tail bank angle.

Figure 4. Flight parameters calculated from 3-D position data

Tail angle of attack from the horizontal was found from the position of the tail apex (y co-ordinate only), the position of the mid tail point (y co-ordinate only), and the tail length between mid point and apex.

Wing bank angle was calculated as the mean of left and right wing bank angles. Wing length was calculated from the position of the wing tip minus the mid wing position. Bank angle was found from the wing tip (y co-ordinate only) minus mid wing (y co-ordinate only) and wing length.

All of the above angle data were subjected to a fourth difference smoothing algorithm.

Velocity was calculated using a parabola fitted to five consecutive points in 3-D space with time (see (Rayner and Aldridge 1985)).

Heading was calculated as the angle between the flight path from position 1 to 2 compared to the flight path from position 1 to 3 (see figure 5). The angle was then calculated from the distance travelled between points 1 to 2 and 1 to 3.

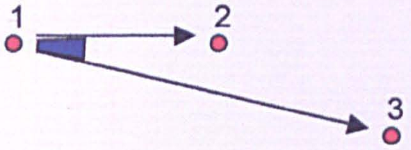


Figure 5. Heading calculation. ● Position of bird, ▰ angle of heading

Heading values are expressed as 180° when straight with angles nearer to 0° and 360° highly curved.

Data analysis methods

Correlations

In total seven different combinations of flight parameters were correlated. Correlations were subject to a Bonferroni correction to account for the increased likelihood of a type I error as a result of multiple correlations on the same data set.

Parameter space.

Correlation predictions were a useful method to begin to consider the data. However, straight correlations represent a simplistic view of these potentially complex interactions. A step beyond correlations would be to predict regions where no data would be expected, i.e regions of performance one would not expect the bird to function in when producing lift. An example of a possible prediction is illustrated in figure 6.

Rates of change

From the parameter data rates of change of tail spread, angle of attack, tail bank angle and heading were calculated. A change was defined as an alteration of the tail or direction of the bird of greater than 10° between frames. The rate was expressed as the number of changes per second

Predictions

Two alternative hypotheses were proposed with regard to potential functions for the avian tail with reference to Thomas' (1993b) work.

The hypotheses were:

1. The tail produces consistent lift to supplement wing lift.
2. The tail provides control during flight.

For each hypothesis predictions were made concerning relationships between various flight parameters in terms of correlations, missing parameter space, rates of change and changes over time.

Hypothesis 1. The tail produces consistent lift to supplement wing lift.

Correlations

If the tail functioned as a consistent lift producing surface various correlations could be predicted (Thomas 1993b). These predictions are given in table 1. If the tail functioned as a consistent lift producing surface, maximum lift production during slow flight would be achieved by the tail being held at the maximum angle of attack possible with the tail as widely spread as possible (Thomas 1996a), tail spread and angle of attack would be positively correlated. Tail spread and angle of attack would be negatively correlated with velocity (Thomas 1996b). Wing bank angle would be expected to be positively correlated with tail bank angle and spread. Tail bank angle would be positively correlated with tail spread and angle of attack (Thomas 1993b; 1996b).

Parameter space

Predictions of areas of unoccupied parameter space were made with regard to each of the correlations consistent with the tail functioning as a lift producing surface (figure 7). If a bird's tail produced consistent lift the relationship between spread and angle of attack would be predicted to be a positive one. Maximum lift is produced by a tail that is spread to its maximum extent at the highest possible angle of attack (Thomas 1996a; b). However, it is also predicted that angle of attack will be reduced before tail spread (Thomas 1996a). This leads to the prediction that there will be an area of parameter space which the bird does not occupy (high angles of attack and low tail spread) (figure 7 a.) Wing bank angle and tail bank

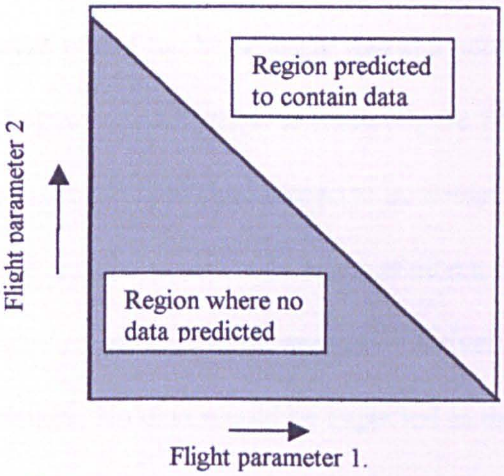


Figure 6. Example of a possible prediction with regard to missing parameter space.

	lift	Control
spread v tail bank angle	+	no relationship
spread v wing bank angle	+	no relationship
tail bank angle v wing bank angle	+	no relationship
spread v angle of attack	+	no relationship
velocity v angle of attack	-	no relationship
velocity v spread	-	no relationship
tail bank angle v angle of attack	+	no relationship

Table 1. Predicted outcome of correlations between seven flight parameters measured from free flying gliding Harris' hawks

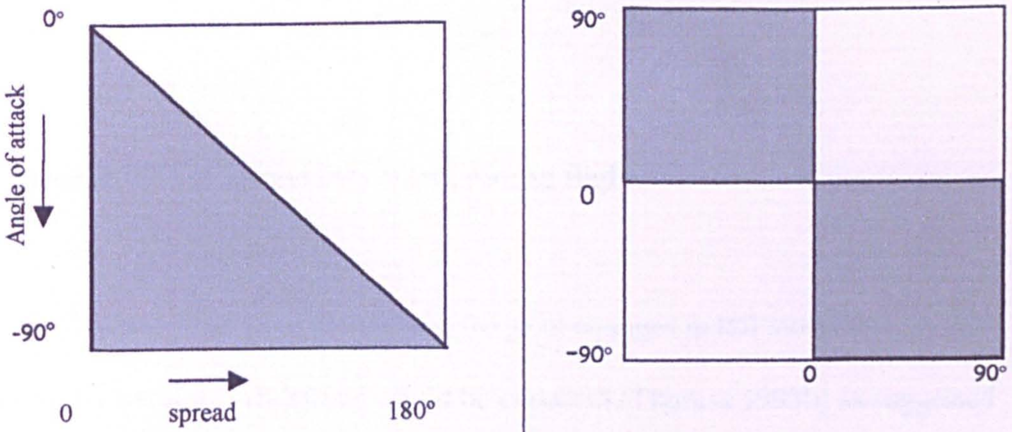
angle would be predicted to be positively correlated. In addition forces would not be expected to act in opposing directions. This leads to the prediction that no data would be found in areas where tail bank angle was at a positive angle and wing bank angle was at a negative angle and vice versa (figure 7 b.). Velocity in relation to angle of attack and spread angle is predicted to be a negative relationship with no values expected at high velocities and high angle of attack or high spread angle (Thomas 1996a) (figure 7 c and d.). Bank angle is positively correlated to tail spread and angle of attack. No data would be expected in the region of low spread or angle of attack and high bank angle. As bank angle increases maximum force would be expected in terms of lift production and thus maximum spread and angle of attack. However, data would be expected at high spread angles and high angles of attack and low bank angles as the tail is utilised throughout flight to produce lift and not solely during turns (figure 7 e and f.). This is applicable to both positive and negative bank angles, negative bank angles would give a mirror image of the graphs shown here (figure 7 e and f) representing a positive correlation.

Rate of change

It would be predicted that changes in spread, angle of attack and bank angle would be infrequent. If the rates of change of heading (direction of flight) were of a similar magnitude to the rate of change of tail spread, angle of attack and bank angle it would be indicative of the tail functioning as a means of consistently producing lift during changes in direction.

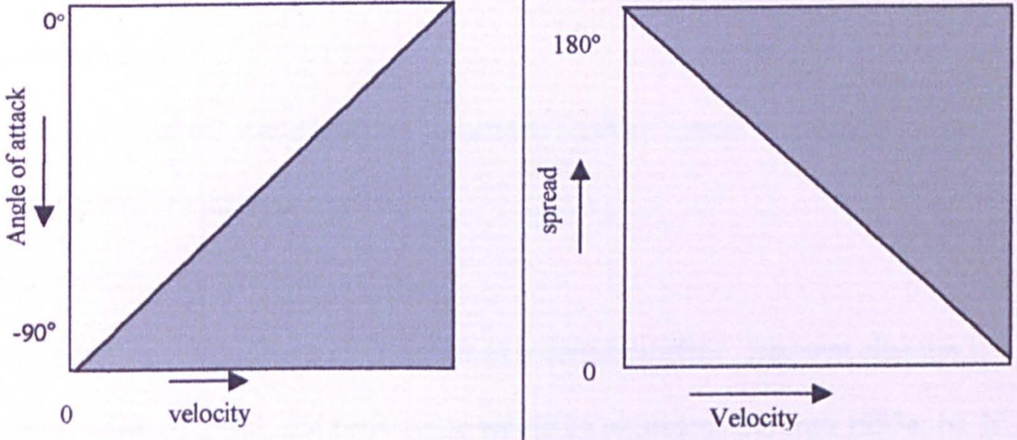
Change over time

Consistent correlations between flight parameters would be predicted if the tail was used to influence the flight path. For example a change in direction consistently being correlated with a change in tail spread.



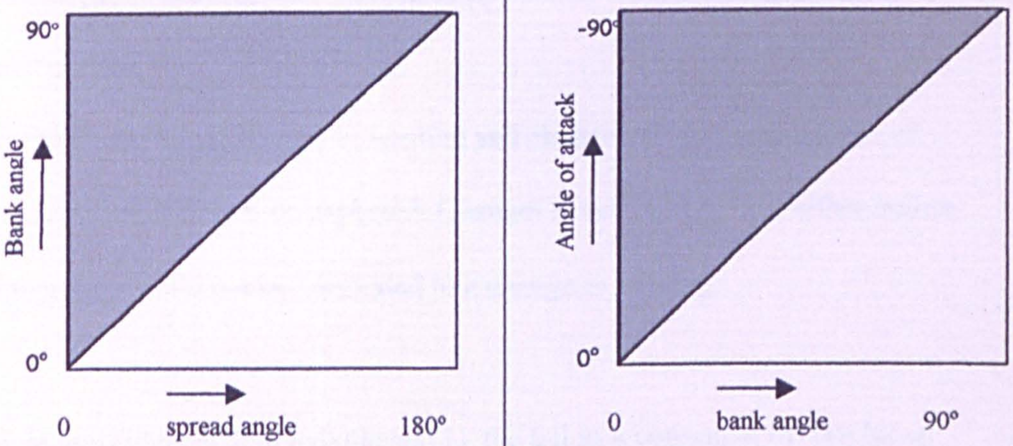
a) Spread v angle of attack

b) Tail bank angle v wing bank angle



c) Velocity v angle of attack

d) Velocity v spread



e) spread v bank angle

f) attack v bank angle

Figure 7. Predicted missing parameter space.
(Grey areas predicted to contain no data points)

Hypothesis 2. The tail provides control during flight.

Correlations

If the tail functioned as a control surface frequent changes in tail morphology with no overall significant correlations would be expected (Thomas 1993b) as suggested in table 1. Correlations may exist momentarily as the tail would produce lift for short periods to provide control but no overall trend should be found.

Parameter space.

No overall correlation would be expected and as such no region of missing parameter space would be predicted.

Rates of change

It can be predicted that if the tail functions as a control surface, frequent changes in tail spread, angle of attack and bank angle would be expected (Thomas 1993a; b). If the rates of change of morphology were found to differ from changes in direction (rate of change of heading) then a controlling function would be implied.

Change over time

No correlation between changes in heading and changes in tail spread, angle of attack or bank angle would be expected. Changes in tail morphology either before or during a turn would not be correlated to a change in heading.

The predictions indicate that hypothesis (1), the tail as a consistent lift producer, would be supported if consistent correlations were found between flight parameters and definite regions of parameter space were identified. The rate of change of parameters would be predicted to be low and correlations between flight parameters and heading would be anticipated. If hypothesis (2), the tail as a control surface, was supported no correlations of flight parameters would be found and no regions of missing parameter space would occur. There would be frequent changes of flight parameters over time and no correlation between heading and flight parameters would be found.

RESULTS

In total 40 individual flights were filmed from seven different Harris' hawks, the length of the flights ranged from 6 frames (0.24 secs) to 40 frames (1.6 secs). For each flight smoothed spread angle, angle of attack, velocity, bank angles of tail and wings and heading were calculated (referred to as flight parameters).

Correlations.

Predictions were made about the direction of correlation between the various flight parameters given the two different hypotheses (see methods). Various relationships between parameters were predicted if the tail acted consistently to produce lift. The seven different correlations described in table 1 were carried out on the flight parameter data calculated for each individual flight. Of the seven correlations only two showed significant correlations in over half the flights measured. There was a significant positive correlation between wing and tail bank angle in 22 flights. Tail spread and angle of attack were found to be significantly negative correlated in 26 flights (angle of attack is expressed as a negative value from horizontal, as such the data indicates that spread angles increase as angle of attack increases but this is represented as a negative relationship). Of the other five relationships none were significant in either direction in more than 7 flights. An exact binomial test was applied to the correlation results and found only tail spread versus angle of attack to be significant (p=0.0403). A binominal test formally tests whether the number of significant results differs from that expected due to chance alone (a close to 50:50 ratio of significant to none significant results). The presence of only one consistently found correlation, that of spread angle and angle of attack, is indicative of the tail functioning as a control surface, hypothesis (2), which predicts no overall correlations.

Parameter space

The seven relationships were plotted and areas of missing parameter space assessed in relation to the predictions in figure 7. No difference in overall pattern in the data was detected between flights or individuals, thus all data was plotted together (figure 8).

Bank angles.

Most of the flights filmed were of birds in straight flight, this is reflected in the results shown in figure 8 b, e, f, and g. Most of the bank angles recorded where less than 30°. All values of tail spread and angle of attack were recorded within the limited bank angle range measured, this may support hypothesis (2) showing no relationship or may be a product of the lack of turning flights measured. The comparison of wing bank angle v tail bank angle reveals an overall trend in line with the predictions of hypothesis (1), however some data points were recorded in the regions of the graph predicted to be areas of missing parameter space by hypothesis (2) (figures 7b and 8b).

Spread and angle of attack.

The comparison of spread with angle of attack shows a clear region of missing parameter space which matches the predict region, no values were measured with low angles of spread at high angles of attack (figures 7a and 8a).

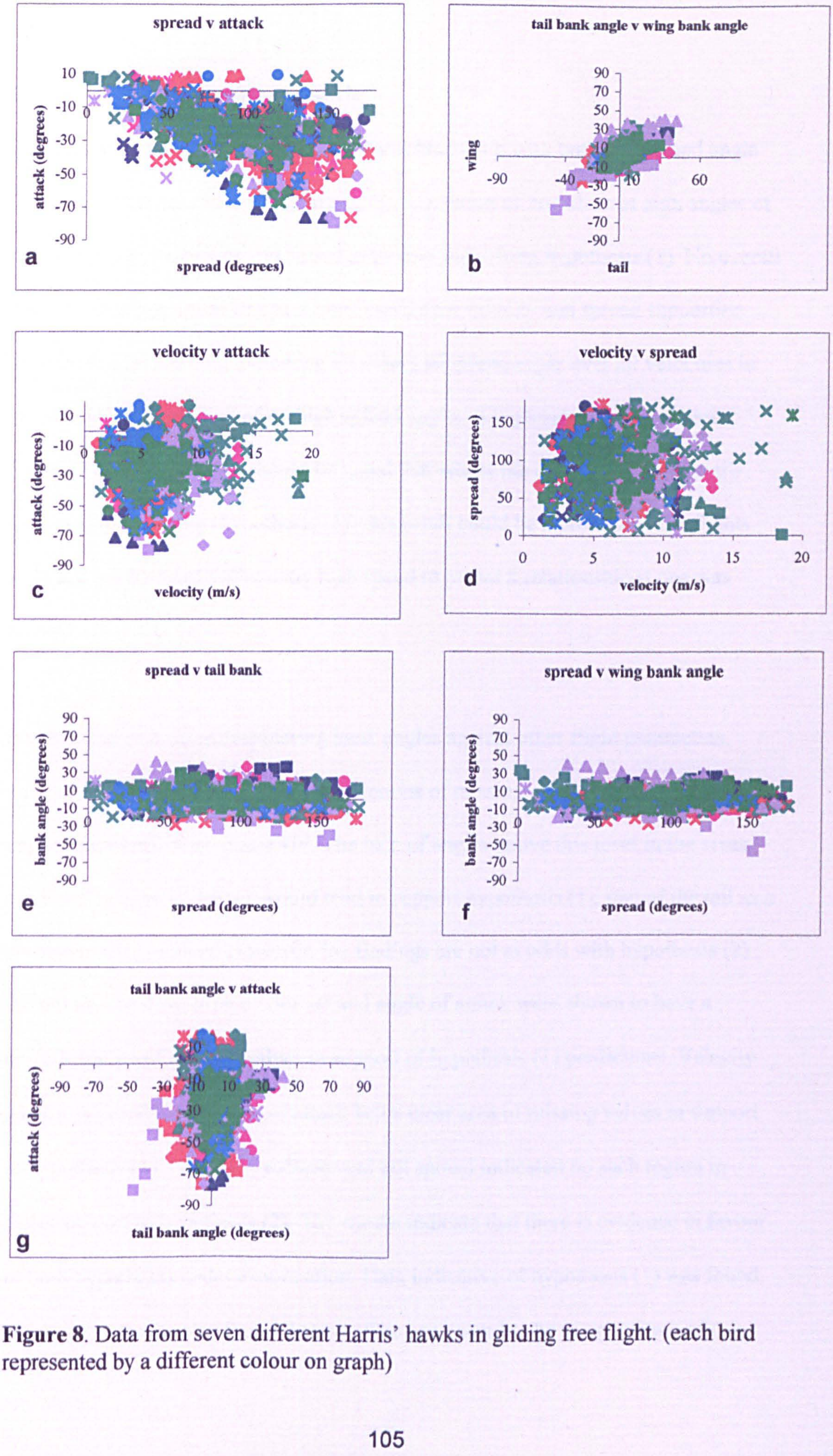


Figure 8. Data from seven different Harris' hawks in gliding free flight. (each bird represented by a different colour on graph)

Velocity, spread and angle of attack.

Velocity was predicted to have a negative relationship with both spread and angle of attack. In the case of angle of attack the prediction of no values at high angles of attack and high velocities was found to be true supporting hypothesis (1). No overall trend of missing parameter space was found with velocity and spread supporting hypothesis (2). The data indicating all values of spread angle over all velocities in contrast to the prediction of no high spread angles at high velocities (Contrast figures 7 c,d and 8 c,d). It should be noted that whilst the data does not show the predicted relationship (hypothesis (1)) this result could be a product of the flights recorded not being of sufficiently high speed to reveal a relationship if one was present.

It was found that when considering bank angles against other flight parameters, most of the data in the area where predictions of missing parameter space were applicable where in an area ± 40°. The lack of angles above this level in the areas predicted to have no values would tend to support hypothesis (1), that of the tail as a consistent lift producer. However, the findings are not at odds with hypothesis (2), the tail as a control surface. Spread and angle of attack were shown to have a definite region of missing values in support of hypothesis (1) predictions. Velocity when compared to tail angle of attack had a clear area of missing values in support of hypothesis (1). However, velocity and tail spread indicated no such region in direct support of hypothesis (2). The results indicate that there is evidence in favour of both hypotheses under examination. Data indicative of hypothesis (1) was found. However, data was also found that could be considered to be in opposition of the predictions associated with this hypothesis. Evidence that the tail produces lift does not contravene the predictions of hypothesis (2).

Rates of Change

Measured rates of change of flight parameters were considered to be high with frequent changes over time (table 2).

Flight parameter	Mean number of changes per second	s.d.
Spread	17.26	6.35
Angle of attack	13.87	4.27
Bank angle	6.44	5.09
Heading	10.75	6.32

Table 2. Rates of change. (change >10° between frames, n=40)

The changes in spread and angle of attack were compared with rates of change of heading no significant differences in rates of change of tail orientation and heading were found as indicated by the standard deviations in table 2. A change in direction of 10 degrees represents a relatively small change in heading during flight, such a change may therefore suggests small adjustments in direction. As change in heading increases above 10° the rate of change decreases, at changes >50° the rate of change had dropped to 5.21 changes per second. This dropping off of rate of change when the magnitude of the change criteria is increased indicates that whilst small changes are frequent, changes of larger magnitude are less so. The data indicates that rates of change of heading, attack, spread and bank angle are of a similar magnitude. This is consistent with the prediction of hypothesis (1) the tail as a lift producer.

However, the rates of change are also considered to be frequent which would be consistent with the tail functioning as a control surface, hypothesis (2).

Changes over time

The relationship between changes in heading (expressed as deviations away from a straight flights path (180°)) and changes in tail spread, angle of attack and bank angle over time was investigated. It is possible that a lag occurs between either a change in heading and the reaction of the tail or a change in tail shape and a change heading. In order to investigate possible correlations between the three tail parameters and the bird's heading and the possibility that these effects were offset over time, a series of correlations was carried out. Each of the tail parameters (spread, angle of attack, bank angle) was correlated with deviation in heading. In addition to this each correlation was repeated but with a lag introduced to investigate a possible time effect. Each data point was thus correlated with the equivalent time data point and with data points 1,2 and 3 time steps in either direction. These steps represented a data point 1/25th, 2/25th and 3/25th of a second earlier and later in the time series. This allowed an assessment of whether heading influenced tail spread, angle of attack and bank angle up to 3/25th second later and whether each of these parameters influences heading on the same time scale. In this way deviation of heading were correlated with tail spread, angle of attack and bank angle for all flights from each of the seven individuals, a total of 120 direct time correlations. In addition each correlation was carried out on time offset data, a total of 720 correlations. Of the 840 correlations carried out 3% showed significant negative correlations and 4% showed significantly positive correlations. Of the significant correlations there was no overall pattern observed. Significant correlations occurred equally over all time lags and were spread over all individuals. This result indicates that there is no consistency of changes of bank angle, spread or angle of attack with heading which would be expected if the tail functioned as a lift producing surface. The lack of significant correlations between the three parameters tested and heading is indicative of the tail functioning as a control surface rather than a consistent lift producer.

DISCUSSION

Harris' hawks were filmed in gliding free flight to begin to assess the validity of two proposed aerodynamic functions for the avian tail. These functions were:

1) The tail produces consistent lift to supplement wing lift (Hypothesis (1)).
2) The tail provides control during flight (Hypothesis (2)).

Predictions were made about the expected relationships between various flight parameters measured from 3-D reconstructions of birds in flight that would be consistent with each of the two hypotheses.

Correlations

Of the seven predicted correlations only a positive relationship between tail spread and angle of attack was significant. Of the other predicted relationships 6 out of 7 were not consistent with hypothesis (1). The general look of correlations between flight parameters was consistent with hypothesis (2). Consideration of correlations between flight parameters represents a starting point from which to begin to differentiate between the two hypotheses. However, a more in depth consideration is required when considering such a complex issue as tail function.

Parameter space

Predictions were made about regions of missing parameter space in addition to the basic predicted correlations. These predictions were then compared to the data to assess the validity of each of the hypotheses. Comparisons of bank angle data with flight parameters revealed most of the data to be in the region of <30°. The overall trend of the data was that of a positive correlation with little data in areas that would convincingly refute hypothesis (1). Small adjustments such as those observed in the region of <30° would be consistent with hypothesis (2). However, the lack of any data at higher angles in areas of predicted missing parameter space give more support to hypothesis (1) than hypothesis (2). Tail spread and angle of attack indicated results consistent with hypothesis (1) predictions with a clear region of absent data. No data were recorded at high angles of attack and low angles of spread. In terms of lift production, lift is determined only by a tail's maximum continuous span which is a derivative of the tail's spread. This may lead to decrease in tail spread being avoided for as long as possible. Because maximum continuous span changes proportionally to tan(spread angle) at high angles of spread smaller changes have more influence on lift production than similar changes at smaller angle of spread. The effect of changing spread angle on lift is thus more pronounced when the tail is fully spread. In addition, Thomas (1996a) suggests a decrease in angle of attack may be a more effective way to reduce induced drag on the tail than decreasing the tail's spread. The differing considerations of the role of spread and attack in lift production is of interest when considering velocity in relation to these two parameters. It is predicted that hypothesis (1) would be supported by a region of missing values at high velocities and high spread and high angle of attack. As speed increases drag associated with angle of attack and spread should be minimised. The results support the prediction of hypothesis (1) with regard to tail angle of attack but not spread, suggesting that angle of attack represents a more restricting feature of tail morphology than tail spread. In terms of the two hypotheses and missing parameter space predictions, whilst some of the data provides supporting evidence for hypothesis (1) the data do not refute hypothesis (2) as an explanation of tail function. Correlations between flight parameters fail to provide convincing supporting evidence of hypothesis (1) whilst finding no evidence to refute hypothesis (2). Consideration of missing parameter space provides some supporting evidence of hypothesis (1) but again hypothesis (2) has not been disproved. Whilst hypothesis (1) predicted definite relationships in terms of correlations and regions of absent data, hypothesis (2) is predicted to show no overall trends.

Rates of change

In order to begin to further disentangle hypothesis (1) and (2) rates of change of flight parameters were considered. Hypothesis (1) predicts changes in spread, attack, bank angle and spread to be infrequent, these changes are predicted to be of a similar magnitude. Hypothesis (2) predicts frequent changes in tail spread, angle of attack, tail bank angle and heading, the changes are predicted to be of differing magnitude. It is difficult to determine whether a rate of change is frequent or not with no yard stick to compare it to. I consider these rates of change to be frequent when considering a bird in flight. The frequent changes in spread and angle of attack are consistent with the tail functioning as a control surface and this hypothesis cannot be refuted. However, the data presented here provides more convincing evidence of the tail functioning as a consistent lift producer with rates of change being of a similar magnitude.

Change over time

The relationship between a bird's flight direction (heading) and tail morphology over time was considered. If heading was influenced by tail morphology such as spread and angle of attack hypothesis (1) would be supported. Correlations between heading and tail parameter being indicative of the tail functioning as a lift producing surface. No correlations were found between heading and tail parameters which supports hypothesis (2), that of small changes of tail morphology unlinked to any consistent change in heading of the bird.

The data presented here indicated that there is evidence to support both of the hypothesis under consideration. Due to the nature of the predictions associated with hypothesis (2) and the tendency for the emphasis to be on no observed pattern, it is difficult to find evidence to refute it. The rates of change providing the only evidence opposing this hypothesis with rates of change of parameters being found to be of a similar magnitude. One of the problems associated with differentiating between the two hypotheses is the likely role of lift production in providing control. These two hypothesis represent a starting point to begin considering the question of tail function but it is likely that they do not represent mutually exclusive functions. The correlation results would seem to support the tail functioning as a control surface, as do the results of the data on change over time. However, data on rates of change provide evidence of the tail functioning as a consistent lift producer. Evidence from the predicted missing parameter space data provides evidence of both control and lift production. From this work it has not been possible to definitively refute either of the hypothesis under scrutiny.

Thomas's (1993a) theory of the forces acting on the birds' tail represents the widely accepted current theory of how the tail produces lift. However, recent work on birds' tails suggests that there are a number of problems associated with the tail functioning as a delta wing as discussed earlier. Work on starling (*Sturnus vulgaris*) in a wind tunnel found that none of the available models used to predict lift on an avian tail were adequate, overestimating lift production. Indeed Thomas's model was found to be the least accurate of those tested (Maybury *et al.* 2001). When watching birds in flight continuously adjusting tail shape and angle it seems likely that the tail functions as a control surface. The data presented here did not allow the two hypotheses under consideration to be convincingly separated.

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CHAPTER 6

Discussion.

Since the first writings of Darwin (1859; 1871) the distinction between, and the importance of natural selection and sexual selection has been a constant subject of research and discussion. Natural selection is selection in terms of survival and is described as the preservation of favourable individual differences and the destruction of detrimental ones. Sexual selection is the mechanism behind the evolution of traits involved in mate choice. Sexually selected traits provide an advantage over conspecifics of the same sex solely with regard to obtaining mates.

In recent years the evolutionary development of avian tails has been subject to much examination and debate. Whether a tail is the product of natural or sexual selection has been at the centre of research and discussion. One potentially naturally selected role for the avian tail would be an aerodynamic one.

The tail streamers of the barn swallow (*Hirundo rustica*) have been the subject of much controversy in recent years. Moller et al. (Møller *et al.* 1998) have shown that tail streamers play a role in mate choice with females preferring long tailed males. However, the streamers have also been shown to play an aerodynamic role during flight (Buchanan and Evans 2000; Evans and Thomas 1997).

It can not be disputed that the elongated tails of some birds represent sexually selected, mate choice ornaments (e.g. long-tailed widow bird (*Euplectes progne*) (Andersson 1982). However, it is becoming increasingly evident that natural selection for an aerodynamic role represents a major influence in tail elongation and should not be overlooked.

A number of potential aerodynamic roles have been proposed for the avian tail, such as increased manoeuvrability and aerodynamic efficiency. Such aerodynamic functions would provide a mechanism through which natural selection could operate. Manipulation experiments can be utilised to look for aerodynamic costs associated with changing tail length and to distinguish between natural and sexual selection (Evans and Thomas 1997). It is hypothesised that a naturally selected structure is present in its optimal form. A sexually selected structure has been extended beyond this naturally selected optimum. In the case of tail length, if an elongated tail is a product of sexual selection through mate choice and thus extended beyond the naturally selected optimum, decreasing the tail length back towards the naturally selected optimum would lead to a decrease in costs associated with the tail. If natural selection is the mechanism behind the observed natural tail length elongation such a decrease would be expected to increase costs.

There is a widening acknowledgement that sexual selection may not be the only mechanism leading to tail elongation. The development of techniques for testing hypotheses concerning aerodynamic roles have allowed potentially naturally selected structures to be investigated in more detail (e.g. barn swallows (*Hirundo rustica*) (Buchannan and Evans 2001)).

Any study of the aerodynamics of birds is greatly complicated by the complexity introduced by the inherent flexibility of a bird in flight. A bird has the ability to make innumerable small adjustments to both body and tail shape whilst on the wing. These movements of a living bird add another unpredictable dimension to any study of flight. The variability of body movements and interactions between various parts of the bird and surrounding air lead to the necessity to simplify the problem in some way. In the first instance this can be achieved to some degree by concentrating purely on gliding flight thus removing the complexity of flapping flight. In addition, the bird can be broken down into its component body parts and the aerodynamics of specific areas studied. The use of model birds whether in component parts or as a whole represents an extremely useful means of controlling some aspects of the equation. This allows a clearer picture of specific aspects of flight to be obtained. The ideal is clearly to use living subjects however this introduces numerous unknown or immeasurable factors into the puzzle, which could mask real effects. A combination of approaches may represent the best method of meeting the problems associated with such a complex subject.

During this study a number of different approaches were used to investigate the question of whether graduated tails were indeed elongated through natural selection for an aerodynamic role. In addition to this the only current theory of how the avian tail functions during flight was tested through the use of stereo video of free flying Harris' hawks (*Parabuteo unicinctus*).

It seems likely that tails of different shapes could be elongated through natural selection to provide different specific aerodynamic functions. The ecology and behaviour of a bird may influence the exact nature of the aerodynamic function that a bird evolves or indeed whether the tail performs an aerodynamic function at all. Birds that migrate long distances may have developed tails that are specifically designed to optimise energy consumption. Efficient lift production could reduce the energy required for sustained flight over long distances. Aerial hawkers may have tails designed specifically to increase manoeuvrability thus optimising hunting efficiency (Norberg 1994). Thus specific tail shapes may be designed to perform quite different aerodynamic functions or may represent a compromise between aerodynamic and ecological constraints.

It has been suggested for a number of years that the tail may play an important stabilising role during gliding flight (Alexander 1971; Evans and Thomas 1992; Hummel 1992; Thomas 1996; Tucker 1992). However, little work has been carried out to investigate to what degree this function is applicable to the tail. A passively stabilising role has been envisaged for elongated tails. This would provide a naturally selected mechanism through which elongation could occur. The current study investigated a stabilising role for elongated graduated tails in male and female adult ring-necked pheasant (*Phasianus colchicus*) through the use of model birds. Manipulation experiments were carried out to alter tail length whilst keeping the overall shape of the tail the same. Pitch stability being assessed by the time taken to regain stability following a destabilising event. Dead birds were deflected from a stable horizontal glide and the time taken to return to the original position measured. The results indicated that both increasing and decreasing the tail length away from the length which naturally occurs, leads to a decrease in the bird's pitch stability. This represents experimental evidence that avian tails may play a major role in the maintenance of stability during gliding flight. The tail length of pheasants was shown to be at a naturally selected optimum in terms of stability. The results found represent the first indication that the widely accepted assumption that pheasants' tails were the result of sexual selection might not be the whole story. Evidence of a stabilising role for the avian tail represents the first suggestion that the graduated tail may have an aerodynamic function. There is a possibility that other species that exhibit an elongated graduated tail, thought to be far from the aerodynamic optimum in terms of lift production, may be a result of natural selection for a completely different function. The pheasant study used model birds and thus did not consider two potentially important factors. Firstly the role of intricate body and tail movements by the bird, secondly effects of a birds behaviour. However, this represents a good first step towards assigning an aerodynamic function to this shape of avian tail. To continue this investigation of potential aerodynamic functions of elongated graduated tails a further experiment was carried out involving living birds.

Magpies (*Pica pica*) were reared in captivity from chick to adult and used in gliding flight experiments to assess the effects of changing tail length on glide performance. Birds' were encouraged to glide the length of a flight cage from perch to food. Tail length was manipulated, again maintaining the overall shape of the tail. Both elongation and reduction of tail length was carried out. Data on flight performance, measured as the relationship between glide angle and velocity, was collected using video cameras. It was found that alteration of the tail length away from the naturally observed tail length led to a significant decrease in a birds ability to glide below specific glide angle and velocity combinations. When birds' tail lengths were modified the range of angles and velocities over which gliding flight could be maintained over flapping flight was reduced. It is possible that this decrease in glide performance resulted from a decrease in stability caused by the increase or decrease in tail length. This interpretation would need further examination as the experiment only explicitly tested a bird's glide performance rather than specifically stability. Recent work on frozen starlings (*Sturnus vulgaris)* in a wind tunnel suggests that furled tails function as a splitter plate and wedge playing an important role in minimising drag during flight. It was found that tail removal led to a sizable and permanent increase in drag (Maybury and Rayner 2001). It is possible that the observed tail length of magpies represents some form of optimum in terms of drag reduction. Maybury and Rayner's (2001) work only investigated the effects of tail reduction on drag. It seems likely that tail elongation will also have consequences in terms of drag. As such, the magpies tail may represent a tail length which minimises drag. This work provides evidence to support the view that elongated graduated tails perform aerodynamic roles and are, at least in some instances, a product of natural selection as oppose to sexual selection.

The evolution of graduated tails and their role during gliding flight was further investigated through the use of comparative analysis. This technique was used to assess whether graduated tails and the advent of gliding flight showed correlated evolution as a result of the graduated tail providing stability. This was not found to be the case but when further investigation of the potential influence of both ecological and morphological factors were take into consideration, correlated evolution between tail elongation and the graduated tail shape was found. It was shown that graduated tails were significantly more likely to be elongated than non-elongated. Tail elongation has been suggested to be a means by which stability can be increased (Hummel 1992). However, this study does not provide any direct evidence of a link between graduated tails and stability.

Thomas (1993) suggested that graduated tails represent the least aerodynamically efficient tail shape. This was based on the assumption that the main role of the tail was one of lift production. In terms of maximum lift production graduated tails may well represent the least efficient tail shape. However, it is still likely that tails provide stability during flight through some degree of lift production. Thomas (1993) suggested the current theory of how the avian tail produces lift and how the tail functions during flight. His work assumed that the avian tail approximates to a delta wing and as such standard aeronautic theory can be applied to explain the forces acting on the tail. The assumptions of the theory are discussed in detail in chapter 5 and will not be revisited here. Work carried out in this study aimed to begin to test Thomas' (1993) theories of tail function and lift production through the use of stereo video on free flying birds.

The work was based on Harris' hawks (*Parabuteo unicinctus*) and used the relationship between various flight parameters to assess the role of the tail during flight. This work aimed to contrast two main hypotheses, that the tail functions as a consistent lift production surface or that the tail functions as a control surface. A control surface would be characterised by rapid changes in flight parameters such as tail spread and angle of attack unrelated to a bird's heading. Lift production would lead to definite correlations and regions of parameter space where no data was recorded with respect to spread, angle of attack and bank angle. The results of this study were not conclusive. Whilst some of the evidence pointed towards the tail functioning as a control surface, the tail functioning as a consistent lift producer was also supported. It seems likely that control would be provided at least partially by lift production. It is perhaps the case that the two proposed hypothesis are not mutually exclusive making distinguishing between them difficult. However, recent work both on delta wings in wind tunnels (M. Evans pers.com) and on Starlings *(Sturnus vulgaris)* (Maybury *et al.* 2001) points to the fact that the tail does not produce lift in the way suggested by Thomas (1993). It is likely that the tail does produce lift in addition to that produced by the wings however the exact mechanism behind this lift production remains unclear (Maybury *et al.* 2001).

The work presented here provides evidence for the tail functioning as a stabiliser during flight and it is likely that the tail also performs other aerodynamic functions, whether they be lift production or control. If Thomas' (1993) theory of the forces acting on the birds tail is eventually rejected, which seems likely in the face of accumulating evidence, all the assumptions about tail shape as related to function would have to be re-examined. This work suggests that the tail may play a stabilising role when graduated and presents an alternative function for a tail shape far from the aerodynamic optimum in terms of lift production (Balmford et al 1993). If we reject Thomas' (1993) view of tail function then all the subsequent predictions on tail shape as associated with tail function must also be discounted. Tail shape may not be restricted by aerodynamic function. Clearly tail length is naturally selected in terms of stability as indicated by work presented here on pheasants and magpies. However, is the tail shape under the same evolutionary mechanism? Do the results here refer to tail length independently of tail shape? Was it solely the tail length of the pheasant and magpie that was at an optimum for stability rather than the combination of length and shape? Does a graduated tail represent the most stable tail shape as oppose to other possible shapes? Thus the question of whether graduated tails provide optimum stability has not been resolved. These are questions that require further work.

The role of natural selection for superior aerodynamic performance represents an important line of enquiry. Equally the role of sexual selection in tail elongation and elaboration remains an important one. This work clearly implicates natural selection as an evolutionary mechanism, natural tails representing an optimal in terms of stability (pheasant) and glide performance (magpie). The question of natural selection versus sexual selection represents a very complex issue with a large number of influential factors that must be taken into consideration. The possibility of both natural and sexual selection playing a role in tail evolution was highlighted in the barn swallow. Elongation was shown to be initially a result of natural selection with further elongation beyond the naturally selected optimum through sexual selection in the male (Buchanan and Evans 2000). What has become clear from this study is that it is difficult to assign any one theory of tail evolution to the elongation of the avian tail. Different tail shapes and lengths may perform different functions as a result of their aerodynamic or mate choice roles. The tail's function during flight is clearly complex and in different situations tails may perform different functions. The constraints defining tail shape evolution are as yet not clearly known. When watching birds in flight the tail provides us with a spectacular geometric display as it continuously alters position and shape. The wide variety of tail shapes, lengths and functions highlight the complexity of nature and the wonder of evolution. It seems likely that in the intricate feat of flight the tail must always to some degree be controlled by aerodynamic constraints. However, it is clear that the exact mechanism and function of the tail and its evolution are as yet not fully understood. It seems likely that the tail performs many diverse functions and is subject to the influences of both natural and sexual selection. The tail has been implicated in mate choice as well as aerodynamic functions such as stability, manoeuvrability and glide performance. At this time we are not in a position to assign any one role to the avian tail. Indeed such an aim is perhaps not a valid one. The tail may be designed to play different roles depending on what is required at the time.

The uniqueness of flight must surely demand a very unique design.

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