# Modelling the evolution of sexual behaviours

A thesis submitted in fulfilment of the requirements
for the degree of Doctor of Philosophy.

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In memory of
Margaret Louise Franklin
(1946-2014)

# Abstract

This thesis presents two studies where natural and sexual selection have interacted to evolve sexual behaviours. The thesis uses mathematical modelling to understand how these forces have caused each behaviour to evolve. This is useful because the results allow for reflection on the potential role of sexual selection in adaptation of these species to a changing environment.

The first study is of early male arrival to spring breeding grounds in migratory avian species, this is termed protandry. The study explores the main hypotheses for avian protandry and then tests the susceptibility of each hypothesis to changing environment.

The second study is of convenience polyandry in species where there is conflict over mating rate. Females have multiple strategies to avoid harassive males but strategies vary in cost and success rate; she must balance her strategy use to minimise her fitness depreciation. The study identifies the main factors that cause convenience polyandry to evolve and paves the way for future studies to investigate if sexual selection over resistance strategy provides these species a future advantage in adaptation to a changing environment.

# Acknowledgments

> *"Remember that with many processes… the most painful moment is right before the breakthrough. So the worse it feels, the closer you must be."*
> MacLeod, 2011

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CHAPTER 1

# Introduction

## 1.1 Introduction

This thesis compares and contrasts two systems where the evolution of sexual behaviours has been shaped by a trade-off between male and female costs. The purpose of this thesis is to reflect on the roles of natural and sexual selection as opposing or complementary forces of selection in each example. Sexual selection may increase a species' ability to adapt to a changing environment which is important as the environment is changing rapidly as a result of human activities (Pomiankowski & Møller, 1995; Lorch et al. 2003; Møller & Szép, 2005; Candolin & Heuschele, 2008; Whitlock & Agrawal; 2009; Spottiswood & Saino, 2010). Understanding the mechanisms of evolution in the two systems explored in this thesis will contribute to understanding the role of sexual selection in species adaptation to changing environments. This will allow identification of those species least able to evolve in the face of climate change and manage our conservation activities accordingly. This work is novel because both studies explore areas of evolution that have a maximum of two existing theoretical modelling studies and very limited empirical understanding.

The first system studied is the evolution of early arrival of male migratory birds to spring breeding grounds. The second system studied is the antagonistic coevolution of harassive male sexual behaviour and resistive female behaviour and the evolution of convenience polyandry. The evolution of both these systems appear to be driven by costs to the male or female and involve trade-offs between natural and sexual selection. The first study is an example of where males primarily appear to pay the costs of mating; males trade off the benefits of a mating advantage they receive through early arrival at a spring breeding ground against the costs of increased mortality as hostile winter conditions linger early in the season. The second study is an example of where females appear to bear the main costs of mating; males will force females into mating and females will resist using different strategies. Resisting and mating is costly to females and they will seek to reduce their costs by strategically surrendering to males who are likely to overcome their resistance anyway. This is theorised to be driven by the female's desire to minimise her costs.

Sexual reproduction is an expensive business; it carries a two-fold cost as well as energetic costs, risk of disease, risk of injury and any costs of parental care (Arnqvist & Nilsson, 2005). It would seem sensible that the optimal strategy for all species is for cooperation within and between the sexes to maximise everyone's fitness. This rarely, if ever, happens. Instead species have evolved traits, behaviours and mating systems that extort and manipulate their mates and each other to maximise their own individual fitness sometimes at the cost of their mate's or population's fitness. The variety of different traits, behaviours and mating systems is remarkable and it is important to understand the selection mechanisms behind as many as possible to identify similarities and increase our overall understating of evolution. This thesis seeks specifically to understand two systems that are examples of inherited sexual behaviours.

## 1.2 Sexual selection

Charles Darwin described sexual selection as 'The struggle between individuals of one sex, generally the males, for the possession of the other sex' (Darwin, 1871). It was the male Indian peacock (*Pavo cristatus)* which Darwin found particularly puzzling with its long, beautiful, brightly coloured tail that females find handsomely alluring yet which makes the male easy for predators to spot and impairs their escape (Gadakar, 2003). There are other seemingly apparent contradictions of natural selection throughout the animal kingdom. For example the male North American moose (*Alces alces)* whose giant antlers used against other males to compete over a female are hugely energetically expensive to grow and hamper his movement, the same is also true in the red deer *Cervus elaphus* (Andersson, 1994). Male guppies (*Poecilia reticulate*) have brightly coloured bellies and elaborate tails that attract both females and predators (Sheridan & Pomiankowski, 1997). Male European starling (*Sturnus vulgaris*) and many other birds sing complex mating songs that advertise their location to females and predators (Zuk *et al.*, 1990; Buchanan *et al.*, 2003). Darwin was confused by many of these examples of sex-related traits which seem to oppose survival but eventually presented the theory of sexual selection to try to explain their evolution (Darwin, 1871).

Contemporary definitions of natural and sexual selection have barely changed since Darwin first presented them. Natural selection is defined as a selective force that acts on any trait or behaviour that affects an individual's competitive ability to survive (Arnold & Wade, 1984, Clutton-Brock, 2007); whereas sexual selection is defined as a selective force that acts on any traits or behaviours that affect an individual's ability to compete for matings (Andersson 1994; Jones & Ratterman, 2009; Kuijper *et al.*, 2012).

Sexual selection originates with the inherent asymmetry in investment that in sexually reproducing species that results in unequally sized sex cells. The definition of a 'male' is the member of the species that carries the smaller sex cells; a 'female' is the one who carries the larger sex cells. Small sex cells are cheap to create and sustain so can be more numerous. Larger sex cells are more costly to produce and so are more limited in number. This difference in number of sperm and eggs creates competition between sperm to fertilise eggs; this is the origin of sexual selection (Kokko *et al.* 2006; Sakurai & Kasuya, 2007; Candolin & Heuschele 2008). Sexual selection is now known to be an important force driving evolution and speciation. The debate of which, natural or sexual selection, is stronger and whether they act together or antagonistically is the focus of much current debate (Rundle et al. 2006; Candolin & Heuschele, 2008; Whitlock & Agrawal, 2009; Spottiswoode & Saino, 2010; Sharp & Agrawal, 2012). Whether sexual selection can drive or speed up adaptation to changing environment like natural selection does is also amongst the most important topics being explored by the evolutionary biology community.

## 1.3 The cost of mating

The cost of the peacock tail to the male was the source of most confusion to Darwin. The concept of costs and benefits of mating to each sex is the focus of this thesis, specifically the costs and benefits of sexual behaviours and how the evolution of these behaviours is driven by natural and sexual selection. There are many species where males receive a high cost of mating, for example the praying mantis (*Mantis religiosa*) and various species of spider (Araneus) whose females are cannibalistic during mating, although these are more extreme cases (Roeder, 1935; Robinson & Robinson, 1980; Elgar & Nash, 1988; Elgar, 1992; Jackson & Pollard, 1997; Judson, 2002). More often females are the sex that receives the main costs of mating. There are many species where females suffer a high risk of death during mating, for example populations of sheep (*Ovis aries*), where males harass females to mate so much and in such large groups females often die of exhaustion and injury (Reale *et al*., 1996; Judson, 2002). Females can also be killed or injured in frogs (*Rana sylvatica*), yellow dung flies (*Scatophaga stercoraria*) and northern elephant seals (*Mirounga angustirostris*) (Banta, 1914; Howard, 1980; Borgia 1981; Boeuf & Mesnick, 1990; Judson, 2002). The female bedbug (*Cimex lectularius*) suffers traumatic injury every time mating occurs as the males pierce the female's abdomen to ejaculate into her body cavity (Stutt & Siva-Jothy, 2001). Costs of mating to females are evident in less extreme examples, for instance males of the fruit fly *Drosophila melanogaster,* who benefit from multiple mating through increased offspring production, have semen which contains chemicals which stimulates oviposition but are also caustic and decrease female longevity. This means while the male appears to receive only benefits from multiple mating, the females of *D. melanogaster* receive benefits but also high costs of mating (Fowler & Partridge, 1989; Chapmen et al. 1995; Lung *et al.* 2002).

In species where multiple mating is beneficial to males and costly to females optimal mating rate should be lower for females than for males. When male and female optimal reproductive strategies are at odds with each other then sexual conflict is occurring

(Parker, 1979). Sexual conflict can result in interesting scenarios of antagonistic coevolution between the sexes where the males evolve traits to increase female mating rate and then female evolve a traits in response to lower her mating rate. Male water striders (*Gerridae*) have evolved 'clasping' appendages and females have coevolved mechanisms to avoid being 'clasped' such as spines or a flattened abdomen (Arnqvist & Rowe, 2002). Sexually antagonistic coevolution may shape behavioural as well as morphological traits. One of my study species, the seaweed fly (*Coelopa frigida*), has males who are highly harassive and will try to coerce females to mate at extremely high rates but females have evolved resistance behaviours to deter them from mating. This is an example of sexually antagonistic coevolution (Dunn *et al.*, 1999; Crean & Gilburn, 1999).

In this thesis I investigate the seaweed flies as an example of sexual conflict where females bear the worst of reproductive costs. Female seaweed flies have evolved multiple response strategies to the males and adjust them according to the costs associated with performing them with different males. What makes this study interesting is that similar evolution of strategy adjustment is exhibited in a wide range of unrelated species including sharks, reptiles, birds, crustaceans and amphibians (Rowe 1991; Crean *et al.* 1999; Cordero-Rivera & Andres 2002; Thiel & Correa 2004; Lee & Hays 2004; Blyth & Gilburn, 2006; Sztatecsny *et al.* 2006; Trontii *et al.* 2006; DiBattista *et al.* 2008; Portroy *et al.* 2008; Adler, 2009; Johnson & Brockman 2010; Griffiths *et al.* 2011). The frequency of this phenomenon across species types makes it all the more important to explore further as it could provide insight into a key evolutionary mechanism. In this thesis I also consider the evolution of early male arrival to spring breeding grounds in migratory avian species. Sexual conflict does not appear to act in this second example but the evolution of arrival dates in each sex are driven by costs and benefits. The differential timing of male and female migratory arrivals is poorly understood empirically and theoretically. Understanding all elements of avian migration is important because understanding how bird populations with different effects of selection on each sex, such as those that exhibit early male arrival, may provide further understanding of how migration generally evolves. Understanding how migration evolves is important because it becomes easier to identify species least able to adapt to changing environments. This can make direction of conservation efforts clearer. It is also important to understand how migration evolves and how climate change may affect the evolution of migratory species because then other negative effects such as damage to agricultural land through changes in bird presence can be mitigated. For example wintering populations of migratory pink-footed geese (*Anser brachyrhnchus*) in Norway have become increasingly numerous as birds adjust their migrations to climate change and they are causing significant damage to farm land in the north of Norway. The damage that these birds cause has become so great the Norwegian government has been forced to introduce a subsidisation scheme to compensate farmers and encourage them to allow the birds to use their land (Eichorn et al. 2009; Tombre et al. 2013; Madsen et al. 2014). If all elements of migration are understood better then scenarios like this could be anticipated better in the future.

## 1.4 Natural selection versus sexual selection

The focus of this thesis is the role of natural and sexual selection as opposing or complementary forces of evolution. Species that exhibit sexually selected traits are hypothesised to be able to react to a changing environment faster than those who are only under natural selection because sexually selected traits often show much greater genetic variation and therefore potential for evolution, than naturally selected traits (Pomiankowski & Møller, 1995; Møller & Szép, 2005; Spottiswood & Saino, 2010). As environments change the balance of the costs and benefits of a sexually selected trait may rapidly change (Candolin & Heuschele, 2008). This makes determining how species will respond to change important. Evidence is also beginning to appear that sexual selection is advantageous because it can prevent harmful mutations from accumulating in a population particularly if the sexually selected trait or behaviour is used by the female to indicate the quality of her mate (Lorch et al. 2003; Whitlock & Agrawal; 2009). The role of natural and sexual selection in the evolution of sexual behaviours is poorly understood and consequently the role sexual selection may play in providing advantages or disadvantages to species that exhibit sexually selected behaviours in adapting to changing environment is not understood at all.

Both of the examples in this thesis show evolution driven by a complex balance of natural and sexual selection and trade-offs between male and female costs; understanding these examples will contribute to the understanding of the role of sexual selection in the rate of evolution and the potential for adaptation to a changing environment in each system. Whether natural and sexual selection work as opposing or complementary forces and whether sexual selection can affect the rate of evolution or provide an advantage to species in adaptation to environmental change is fiercely debated and the work in this thesis will provide an important contribution for our understanding (Lorch et al. 2003; Rundle et al. 2006; Candolin & Heuschele, 2008; Whitlock & Agrawal, 2009; Spottiswoode & Saino, 2010; Sharp & Agrawal, 2012).

First this thesis investigates early arrival of male migratory birds to a spring breeding ground. Migratory bird species already show they are susceptible to environmental changes through their reactions to climate change; perhaps migratory bird species where natural and sexual selection have differential effects on the sexes may show increased resilience to environmental change. To explore this further this thesis first considers the main hypotheses of early arrival in male migratory birds then tests the susceptibility of each hypothesis to environmental change. Perhaps species which show coevolution between the sexes, such as the system here where the female has shown evolution of mating strategy in response to male harassment, already have the evolutionary mechanisms in place to allow them rapid response to changes in the environment. Second this thesis explores the sexually antagonistic coevolution of female mating strategy in species where males are harassive. This study does not directly consider how these species may react to changing environment, however by exploring how the forces of natural and sexual selection interact in these species this work paves the way for future studies to identify any advantages in response to changing environment sexual selection provides them. The more mechanisms of evolution are understood through identifying the roles of natural versus sexual selection as opposing or complementary forces, the easier it will be to predict the role of sexual selection in other species' adaptation to changing environment.

Very little is currently understood about the role of natural and sexual selection in both study systems so it is useful to adopt a theoretical approach initially to analyse the systems and identify where empirical research may be most efficiently utilised. In this thesis I use mathematical modelling as the initial theoretical explorations of both early arrival of male migratory birds and female response strategy to harassive males in insects.

## 1.5 Mathematical modelling of sexual selection

This thesis is a study of the roles of natural and sexual selection in the evolution of sexual behaviours and uses mathematical modelling to explore the study systems of early arrival in male migratory birds and female strategy in insect species which exhibit pre-mating struggles. I now provide an introduction to the use of mathematical modelling for understanding sexual selection. It is useful to note mathematical modelling is infrequently used to explore the evolution of sexual behaviours driven by sexual selection; usually the target is a morphological trait that is under sexual selection.

Mathematical modelling is a useful tool for studying evolution because it provides an ability to simulate an evolutionary scenario and quantitatively test adjustments of balances and trade-offs between parameters. Mathematical modelling has already been used to study natural selection extensively and techniques and examples are readily found in classic textbooks such as Bürger (2000), Murray (2002) and Rice (2004). In this thesis I am concerned with the application of mathematical modelling to evolutionary systems driven by natural and sexual selection, particularly the evolution of sexual behaviours for which mathematical modelling is rarely utilised.

### 1.5.1 This thesis uses a mix of game theory and quantitative genetics

Models of sexual selection are grouped under four categories depending on their different assumptions and approaches; population genetics, individual based simulations, quantitative genetics and invasion analysis. Population genetics is used to track how the distribution of certain alleles changes over time throughout a population (Kuijper *et al.,* 2009). Individual-based simulations are used to create a population of unique individuals and allow them to interact with each other as individuals in real time in a virtual environment. Individual based simulations are very time consuming as many thousands of simulations must be repeated before general conclusions can be reached (Kuijper *et al.,* 2009). Quantitative genetics tracks how the distribution of phenotypes, the physical manifestation of genetic material throughout a population changes, over time. Invasion analysis, including adaptive dynamics techniques, is a type of game theory. A fitness landscape is determined for individuals in the population depending on particular trait values they have and then maps the effect of introducing breeding individuals with small mutations that confer that individual either an increase or decreases in fitness relative to the rest of the population. Adaptive dynamics is becomingly increasingly used to study evolution in systems such as virulence of bacteria and diseases and in the evolution of parasitoid emergence (Romero & Arnold, 2009; Hackett-Jones *et al*. 2011).

This thesis aims to understand how the distribution of behavioural phenotypes within a population change over time driven by male and female strategies developed according to costs and benefit trade-offs. The most appropriate technique for this is game theory. The thesis uses game theory along with the derivation of fitness equations and elements of quantitative genetics. Game theory is appropriate because it allows for cost-benefit trade-offs and strategy development of behaviours of each sex. Quantitative genetic techniques are used when the distributions of behavioural strategy throughout male and female populations of each generation and how they evolve over time is considered. Individual based simulations may have been useful, however game theory is a more efficient method. As Chapter 6 discusses, individual based simulations could be an avenue for future work to reinforce the models presented here. Population genetic techniques are inappropriate for this thesis because I do not aim to understand changes at the chromosomal level.

### 1.5.2 This thesis illustrates the complexities of modelling sexual selection

Models of sexual selection are inherently more complex than models of other forms of selection because of the many extra factors to consider when a population is treated as two interdependent sexes rather than one homogenous mass. Complexity in modelling can be useful because it can increase model specificity but can also be a problem because models with many parameters are harder to analyse and identify underlying mechanisms from. So there is a trade-off in modelling; less complex models may lack realism but allow us to understand fully what each component does and allow a full sensitivity analysis from which the results can become a basis for future empirical research or model development, whereas highly complex models allow for very specific conclusions to be drawn about very specific systems.

In this thesis I present models with a range of complexity levels. The first study of bird migration shows a series of simple models that I use to reflect generally on the mechanisms driving the evolution of male early arrival at spring breeding grounds but the study of female strategy in seaweed flies is much more species specific and as a result is more complex. In the discussion chapter I will reflect on the effects the different levels of complexity had in each study.

### *Trade-offs at the individual level are important in modelling sexual selection*

The first complication modelling sexual selection presents is the need to capture the behaviour of the individual and interpret its effect on the population. This is particularly apparent in this thesis because every model investigates individual to population level effects. Interactions at the individual level may have unexpected effects at the population level because individuals may evolve strategies that maximise their own fitness but these strategies may not necessarily maximise the fitness of their mate or population. Consider a population of two males, A and B, who each invest $x$ resources in reproduction and $1-x$ resources in survival. The probability of mating is proportional to the resources each male invests in reproduction and in this population both males have equal probability of mating. A female chooses randomly and mates with male B, male B sires 2 offspring and male A sires no offspring and the population grows by 2 individuals who each also invest $x$ in reproduction and $1-x$ in survival. Now consider another populations consisting of males C and D. Male C invests heavily in reproduction, $x+\epsilon$ resources, and increases his probability of mating, this comes at a cost to his investment in survival which is now $1-x-\epsilon$ as his resource pool is finite. Male D invests $x$ resources in reproduction and $1-x$ in survival. Due to his increased investment in reproduction male C secures the mating and produces 2 offspring with the female and male D produces no offspring. The population has still grown by 2 individuals but these offspring have inherited a different reproduction and survival resource allocation pattern; the growth rate of both populations is equal but the individuals are different. In particular survival at the population level has decreased to gain the benefit of a higher mating probability at the individual level (figure 1.1).

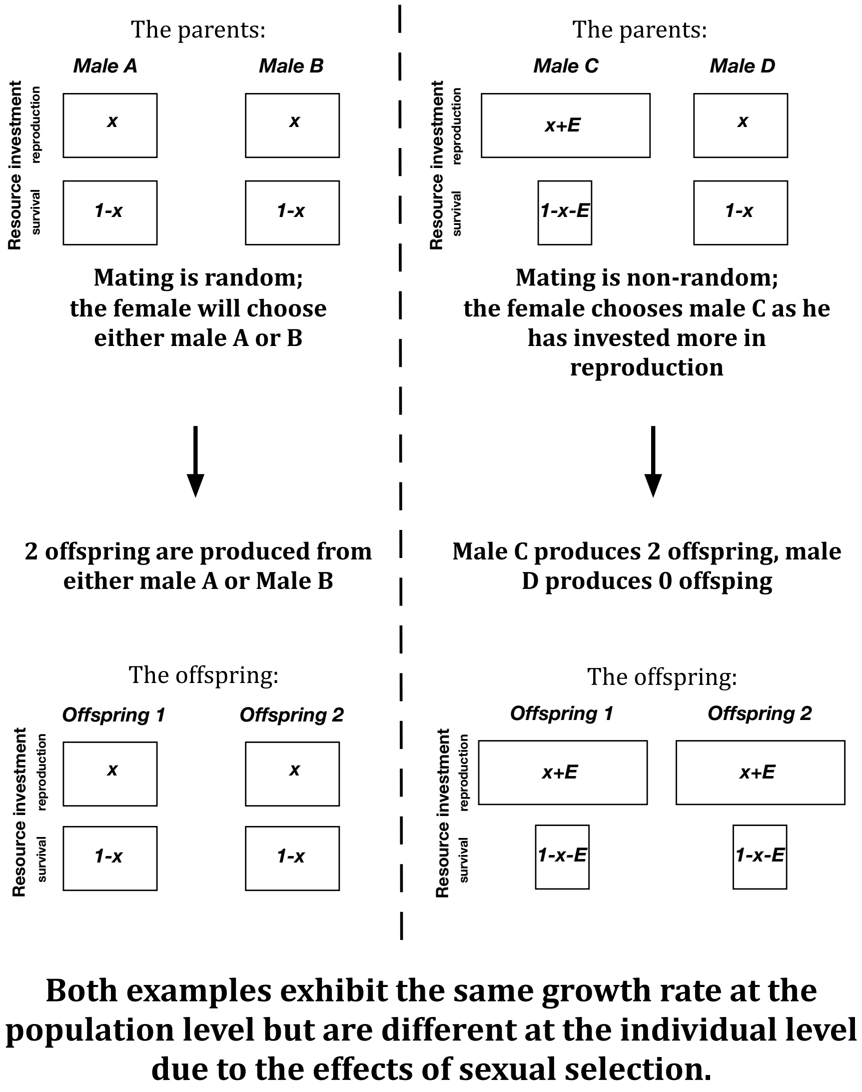

**Figure 1.1 Trade-offs at the individual level have effects at the population level.** An individual can choose to invest in reproduction or survival

### *Further complexities of modelling sexual selection*

To demonstrate some other complexities sexual selection brings to modelling I will use an example of the dynamics of a predator-prey system. The predator-prey example is a classic example usually presented as a population dynamics model. Population dynamics are not commonly used for modelling sexual selection because they show the strategy a population will take to maximise its growth and are unable to show the strategy individuals may choose to maximise their own fitness and reflect on how this affects the population. To explore the population and individual strategies, fitness equations are more appropriate. For this thesis models are built as fitness equations from an individual view point and omit population dynamics.

An example of a population dynamics model of a predator-prey system is:

$$\frac{dQ}{dt} = cPQ - d_Q Q$$

(Eqn 1.1)

$$\frac{dP}{dt} = aP - ePQ - d_P P$$

(Eqn 1.2)

Where $P$ is some measure of abundance of prey and $Q$ of the predator. The parameter $e$ is the rate of predation, $c$ is the rate predators turn prey into offspring, $a$ is the birth rate of the prey and $d_Q$ and $d_P$are the natural death rates of predator and prey (Murray, 2002).

I now derive fitness equations from the predator and prey populations detailed in the model presented in equations 1 and 2. The fitness of a predator species, $W_Q$, and its prey, $W_P$, assuming the equations of population dynamics above hold true might be:

$$W_Q = ceP - d_Q$$

(Eqn 1.3)

$$W_P = a - eQ - d_P$$

(Eqn 1.4)

But what if we want to examine the prey species further? For example in reality the prey species may be sexually dimorphic with males and females predated on at different rates. We assume sexual selection is operating because the male must maintain his bright plumage to attract mates and this is where complications arise. If males are brightly coloured to attract mates this may also make them easier targets for predators, if females are drably coloured perhaps they are better camouflaged from predators. How does splitting one population into two sexes that are predated on at different rates complicate the model?

To demonstrate the effect of modelling sex specific assumptions, such as would be used in modelling sexual selection and will be demonstrated throughout this thesis, the prey fitness equation must be split into two fitness equations, one for the male population, $W_{P:\,Male}$, and one for the female population. $W_{P:\,Female}$:

$$W_{P:\,Male} = \mathrm{A}(\mathrm{P}_M, \mathrm{P}_F) - e_M Q - d_M$$

(Eqn 1.5)

$$W_{P:\,Female} = \mathrm{A}(\mathrm{P}_M, \mathrm{P}_F) - e_F Q - d_F$$

(Eqn 1.6)

The first obvious complication of this model is the extra equation and extra parameters required to accommodate two sexes, parameters $d_M$ and $d_F$ are the natural death rates excluding predation and $e_M$ and $e_F$ are the male and female predation rates. This is a common problem of models of sexual selection where the population has to be divided into two sexes but united as one population whereas in a model of natural selection the population can be treated homogenously (Kujiper *et al.* 2009). The addition of a second equation has moved the focus of the model from simply the number of prey in the population as in the first model to the makeup of the population, how many males and how many females, in the second model. The need for two equations that must be separate but united shows the second complication models of sexual selection may cause; male and female offspring must both be produced, potentially at different rates, and breeding may not continue if one sex goes extinct (Bacelar *et al.* 2011). In the second model $\mathrm{A}(\mathrm{P}_M, \mathrm{P}_F)$ acts as an abbreviated breeding term which may have to account for sex ratios, within sex competition, between sex competitions, costs of mating and competition over investment of energy into offspring (Trivers 1972; Trivers & Willard 1973; Ritchie 2007; Kuijper *et al.* 2009). Compare the $\mathrm{A}(\mathrm{P}_M, \mathrm{P}_F)$ term fitness equations of each sex (eqns 5 and 6) with the second of the population dynamics model (eqn 2) where the breeding rate of the prey could be reduced to a single, simple parameter, $a$.

Further complexities of models of sexual selection which may occur but this example does not illustrate include the complex mechanisms of genetic inheritance and resource allocation trade-offs. Genetic mechanisms are much easier to ignore in other models of selection because they do not consider different traits expressed in different sexes (Lande, 1981; Maynard Smith, 1982; Iwasa *et al.* 1991; Kujiper *et al.* 2009). Trade-offs in resource use, for example allocation to reproduction versus survival and the resulting costs or benefits this produces, are often a subject of models of sexual selection and can become quite convoluted and difficult to model. This is further complicated as the trade-offs may be on the individual level or on the population level and one may affect the other. This model does not include genetic mechanisms but has the potential to be analysed assuming trade-offs between any of the sexual parameters and survival for example.

## 1.6 Introducing the study systems of this thesis

So far this thesis has illustrated that understanding the roles of natural and sexual selection and the interplay between the two forces is important because species that exhibit sexual selection may be at an advantage when it comes to adapting to changing environments. The study systems this thesis considers have been briefly introduced and the thesis has presented the modelling techniques that will be utilised. I will now further discuss the two study systems of this thesis explaining the state of the current knowledge and what I aim to contribute. I will also highlight what makes this work novel and why it is important.

### 1.6.1 Protandry in migratory avian species

#### *The current state of knowledge*

Part 1 of this thesis details my study of the evolution of male and female arrival times to spring breeding grounds in species of migratory birds and how this is affected by climate change. In many avian species males arrive at spring breeding grounds before females, this male-first arrival timing is termed *protandry*. Breeding timing for both sexes is a trade-off between natural and sexual selection, they each must arrive early enough to find a mate and breed successfully but not too early as the breeding ground will still be in a winter condition which may affect their chances of survival on arrival. This is a trade-off between natural and sexual selection through a balance of male and female costs. There are several proposed hypotheses for why males evolve to arrive first including to increase the opportunity they have to mate with arriving females, to secure a mating advantage through claiming a good territory first or because males which generally have a larger body size are less susceptible to poor conditions than females and can survive earlier (Morbey & Ydenberg, 2001). The empirical evidence for each of these hypotheses is conflicting and modelling work to help iron out the details of each hypothesis is very limited. In Chapter 2 I present a series of simple but elegant models that examine each hypothesis individually and in combination to examine the roles of natural and sexual selection through costs and benefits in driving the behavioural evolution of arrival date in protandrous avian species.

The results of the models in Chapter 2 showed that avian protandry is very susceptible to changes in environment. Chapter 3 presents work exploring the effect of environmental change on protandry. It explores how protandry driven by each of the main hypotheses may react as the climate warms and between year environmental conditions become more uncertain.

### *Why this work is novel*

My work presented in Chapter 2 is novel because there currently only exists two models of protandrous avian migration, Kokko (1999) and Kokko (2006), and only the latter considered the evolution of arrival dates of both sexes. Considering the conflicting nature of the empirical studies of the evolution of protandry in migratory birds this is surprising because mathematical modelling would serve a useful tool for ironing out the details of each hypothesis and combination of hypotheses. The models I present in Chapter 2 are novel because they consider more hypotheses than the previous models and in more combinations. The models of Chapter 2 are also novel because they provide an integrated framework of all the hypotheses and consider the distribution of arrival timings throughout the entire population rather than just the mean arrival date.

Other modelling studies do exist on the effect of climate change for example in species such as the bagworm (*Thyridopteryx ephemeraeformis*) who show different emergence dates from the pupal stage for males and females (Lynch et al. 2014). The work presented in chapter 3 is novel however because there are no existing studies that specifically consider assumptions on the migration of protandrous avian species including the interplay of the three main hypotheses for protandry in birds and their interplay; the rank advantage hypothesis, mate opportunity hypothesis and susceptibility hypothesis.

Notably there are also very few empirical studies that investigate the effect of climate change on protandrous species.

### *Why this work is important*

This work is important because it will identify protandrous species most at risk from climate change and so be useful in determining where conservation efforts should be focused to prioritise species protection and because it will provide insight into how sexual selection may affect the adaptation of migratory bird species in response to climate change. Migratory bird species are already demonstrating they are very susceptible to environmental change through advances of whole species arrival dates and changes in migratory routes (Crick et al. 1997; Ivanauskas et al. 1997; Bradley et al. 1999; Crick & Sparks 1999; Butler 2003; Hüppop & Hüppop 2004; Lehikoinen et al 2004; Marra et al. 2005; Rainio et al. 2007; Ruboilinio et al. 2007; Thorup et al. 2007). Understanding the evolutionary mechanisms of protandry in avian migration is important because it explores the role sexual selection has in evolution of arrival dates. This can then provide insight into how differential effects of natural and sexual selection between the sexes may contribute to the response of a migratory bird species to climate change. Chapter 2 allowed me to provide further insight into the possible mechanisms of evolution of protandry and Chapter 3 allowed me to directly consider how the roles of natural and sexual selection may interact to allow the adaptation of protandrous species to climate change.

## 1.6.2 Convenience polyandry in the Coelopids

### *The current state of knowledge*

The second part of this thesis details my study of the evolution of pre-mating struggles in the seaweed flies (*Coelopidae*). The seaweed flies are characterised by a breeding system with very high mating rates (Dunn *et al*. 1999; Blyth & Gilburn, 2006). Males have evolved an aggressive mating behaviour to harass and coerce a female into mating. Females have evolved resistance behaviours of shaking, kicking and abdomen curling when attacked by a male to prevent mating (Crean & Gilburn, 2002). Females are likely to incur costs from both mating and resisting (Meader & Gilburn, 2008). The female response is particularly interesting because they exhibit a behaviour called *convenience polyandry*; usually a female is resistive to all male harassment but when a large male who is highly likely to overcome her resistance response attacks her she submits to his mating. Convenience polyandry is hypothesised to be a way for females to minimise their costs and avoid fights they are likely to lose (Thornhill & Alcock, 1983). In chapter 4 I will present a model of the evolution of female strategy and explore why the evolution of convenience polyandry may have occurred in some species but not in others. Chapter 5 details my subsequent empirical efforts to further develop understanding of factors the model in Chapter 4 identified as key factors in the evolution of convenience polyandry.

### *Why this work is novel*

The work in this thesis on convenience polyandry is novel because it is the first mathematical model of convenience polyandry. It also provides the first attempt, admittedly unsuccessful, in separating the costs of mating and harassment in the seaweed fly.

### *Why this work is important*

Understanding of the nuances of the evolution of convenience polyandry is lacking both theoretically and empirically despite convenience polyandry occurring in a wide range of species throughout the animal kingdom. This work explores the balance of costs and benefits that cause convenience polyandry to evolve and not evolve. The universality of the phenomena indicates that understanding it may provide a large advance in the understanding of evolution through sexual selection generally. Understanding the roles of natural and sexual selection in the evolution of convenience polyandry also paves the way for future work to investigate whether ability of one sex to adapt to changes in the other may provide the entire species with an advantage of ability to adapt to changes in environment.

## 1.7 Summarising the relevance of this thesis

### 1.7.1 A summary of the current state of knowledge

The roles sexual selection and natural selection have on species adaptation to environmental change as either opposing or complementary forces is unclear. Costs and benefits of behaviours and traits cause complexities in understanding the interactions between natural and sexual selection and existence of anomalies such as sexual conflict compound this and make measurement of each force difficult (Spottiswoode & Saino, 2010). The two study systems presented in this thesis are particularly poorly understood, both theoretically and empirically, examples of the role of natural and sexual selection as opposing or complementary forces in the evolution of sexual behaviours. Better understanding of the evolution of the behaviours in these systems and how they are driven by the interplay of natural and sexual selection may ultimately provide insight into the advantages and disadvantages of sexual selection in adaptation to changing environments.

There are only two existing models of avian protandry and no existing models of the effect of climate change on protandry. Empirical studies of migratory avian protandry are limited and empirical studies of the effect of climate change on avian protandry are even scarcer. Despite being a phenomenon that occurs throughout the animal kingdom there are no models of convenience polyandry and no theoretical studies of the potential for species which exhibit convenience polyandry that investigate whether sexual selection may provide these species with an increased or decreased ability to adapt to environmental change.

This thesis presents models of protandry in Chapter 2 and a modelling study of the effect of climate change on protandrous migratory avian species in Chapter 3. The thesis then introduces the first model of convenience polyandry in Chapter 4 and resulting empirical work in Chapter 5 that was designed to provide feedback to increase the accuracy of the model in Chapter 4.

### 1.7.2 The aims of the thesis

The aims of this thesis are specifically:

1. To further theoretical understanding of the evolution of protandry in avian migration and the evolution of convenience polyandry in systems exhibiting male harassment.
2. To reflect on the roles of natural and sexual selection as complimentary or opposing forces in the evolution of protandry in migratory avian species and convenience polyandry.
3. To consider the role of sexual selection in providing advantages or disadvantages in the adaptation of protandrous migratory avian species in response to changing environment.
4. To pave the way for future studies of convenience polyandry to identify the role of sexual selection in providing advantages or disadvantages in the adaptation to changing environment of these species.

### 1.7.3 Why the work in this thesis is important

The work in this thesis is important first because it provides insight into the evolutionary mechanism behind protandrous avian migration and identifies the protandrous species groups most at risk from climate change. This should be used to focus future conservation efforts to minimise the damage climate change could cause to these species. This will also be useful in understanding how migratory birds generally may respond to climate change showing when species may evolve protandry as a response and if protandrous species have an advantage when faced with climate change. The work in this thesis is important secondly because it provides insight into the evolution of a female strategy behaviour that is exhibited through a wide range of species; understanding behaviours that occur frequently in unrelated species may provide large gains in the understanding of mechanisms of evolution generally. Finally the work in this thesis is important because it compares the role of sexual selection in the evolution of two poorly understood examples of sexual behaviour; this contributes to the wider understanding the role of sexual selection generally and provides scope for future work to consider if species that exhibit behaviours such as convenience polyandry or protandry have increased ability to adapt to changing environments.

# Part 1

# The protandrous arrival of migratory avian species at spring breeding grounds

CHAPTER 2

# The protandrous arrival of migratory avian species

## 2.1 Introduction

### 2.1.1 Protandry

The biological scheduling of events in animal life is carefully controlled. Often important life history timings occur earlier in males than they do in females, particularly if it is related to sex. Males of the sheet web spider (*Pityohyphantes phrygianus*) reach sexual maturation before females (Gunnarrsson & Johnsson, 1990) and male insect-parasitic nematodes disperse into new hosts before females (Grewal *et al.* 1993). Male salamanders go back to their breeding pond before females (*Ambystoma talkpoideum*; Semlitsch *et al.* 1993 and *Ambystoma jeffersonianum*; Douglas, 1979) and male common lizards (*Lacerta vivipara*) emerge from hibernation before females when the environment is hotter in what appears to be a bid to use the heat to speed up the development of their sperm and increase the number of mating opportunities they can seize when the females emerge (Van Damme *et al.* 1987). Male sand lizards (*Lacerta agilis*) come out of hibernation on average two weeks before the females (Olsson & Madson, 1996) and male vermillion spotted newts (*Notophthhalmus vitidescens*) arrive at breeding grounds before females (Hurlbert, 1969). Red-sided garter snakes in Manitoba occur in high male biased sex ratios and males leave their underground dens for breeding earlier than females and male ground squirrels come out of hibernation 1-4 days before females in Alberta, Canada (Michener, 1983; Gregory, 1974). Male pacific salmon are frequently found at spawning sites before females (Morbey *et al.* 2000). There are also examples of males acting before females in the reproductive timing of plants (Richards, 1986). This concept of ‘males first’ for arriving, emerging or maturing before females is termed protandry.

Protandry is common amongst migratory avian species where males often arrive at a summer breeding ground before females do. The mechanisms for the evolution of protandry in birds however remain poorly understood. A study of species of trans-Saharan migratory birds showed high levels of protandry and revealed the degree of protandry was strongly associated with the degree of difference between male and female colouration (Rubolini *et al.* 2004). In Ontario, Canada, 18 species of paruline warbler where identified as showing protandry and found the earliest arriving species had the highest degree of protandry (Francis & Cooke, 1986). Another Canadian study of 30 passerines birds suggested the degree of protandry is correlated with differences in male and female size; as the difference between male and female size increases, so too does the degree of protandry (Kissner *et al.* 2003). In Europe, some Palearctic songbird species have been shown to be protandrous in their migrations. It is suggested this could be so males can achieve extra-pair copulations (EPCs), copulations with females other than their mates (Coppack *et al.* 2006; Rainio *et al.* 2007). A study of the Waved Albatross (*Phoebastria irrorata*) showed they too were protandrous and this may be because the males want to achieve EPC (Huyvaert *et al.* 2006). Some shorebirds are protandrous including red phalaropes and sanderlings (*Phalaropus fulicarius* and *Calidris alba:* Myers 1981*)*.

Avian protandry is not fully understood because evidence from different species with different mating systems all suggests different hypotheses for its evolution. This chapter presents mathematical models of the three main hypotheses of arrival timings in protandrous migratory avian species to help establish the most likely mechanisms that drive protandrous migration.

### 2.1.2 Hypotheses of protandry

Six formal hypotheses have been proposed for understanding protandry. The first, the *rank advantage hypothesis*, states early arriving males receive a benefit of securing a valuable, high quality territory due to less competition from other males and more unclaimed territories are available (Ketterson & Nolan, 1976; Myers 1981). The second, the *mate opportunity hypothesis*, states males who arrive at a breeding area before females have increased opportunity to mate with females as they arrive (Morbey & Ydenberg, 2001; Morbey *et al.*, 2012). The third hypothesis, the *susceptibility hypothesis*, states there is some covariance between arrival time and individual quality or condition. If males are generally bigger, hardier and stronger than females and can tolerate poor condition at the breeding ground better than females they can afford to arrive earlier than the female (Fisher, 1930; Møller *et al.* 2008). The susceptibility hypothesis theorises that protandry is driven by the different effects of natural selection on the males and the females (Ketterson & Nolan, 1976; Morbey & Ydenberg, 2001).

The rank advantage and mate opportunity hypotheses are both examples of directional sexual selection pushing the arrival date earlier in the season but are opposed by natural selection pushing arrival date later because of high death rates early in the season at the breeding ground as winter conditions linger (Møller, 2008). Maximising fitness against natural and sexual selection gives the optimal arrival date.

Other hypotheses include the *waiting cost hypothesis* which assumes females migrate or emerge later than males to allow males to mature and minimise time wasted between arrival and breeding (Taylor *et al.* 1998). The *mate choice hypothesis* is where females gauge male condition or quality as a mate by how long he has been able to survive at the breeding ground and the *constraint hypothesis* attributes logistics to the cause of protandry, for example if males winter closer to the breeding grounds than females they could easily arrive sooner in the breeding season. None of these last hypotheses have strong empirical evidence from avian studies to support them however (Morbey & Ydenberg, 2001).

Three of the formal hypothesis appear to be particularly relevant to avian species; the rank advantage, mate opportunity and susceptibility hypothesis. These hypotheses appear to have different support from different species. Spanish Barn Swallows provide evidence that supports both the susceptibility and mate opportunity hypothesis; large, strong males arrive first when conditions are poor and achieve higher fecundity and males that arrive early have higher success rates in preventing their mate from re-mating (Møller, 1994). The Pied Flycatcher (*Ficedula hypoleuca*) is a territorial bird that exhibits protandry, yet it exhibits evidence that supports the mate opportunity rather than the rank advantage hypothesis because territory quality does not actually appear to confer an advantage to them whereas early arrival does (Canal *et al.* 2012). Eastern Kingbirds (*Tyrannus tyrannus*) benefit from early arrival from both ability to acquire a good territory and opportunities to mate early and multiply, supporting both the rank and mate opportunity hypothesis (Cooper *et al.* 2011). Male American Redstarts (*Setophaga ruticilla*) provide evidence to support the rank advantage hypothesis and potentially the susceptibility hypothesis. Males with the biggest tails tend to arrive first and acquire the best territories, females also use a male's tail as an indicator of his quality and social ranking (Reudnick *et al.* 2009). The Waved Albatross (*Phoebastria irrorata*), an apparently monogamous species that mates for life, provides evidence for the mate opportunity hypothesis because the male will seek sneak matings with other females he is not paired with. Early arrival provides him with more opportunities for matings with other females and thus supports the mate opportunity hypothesis (Huyvaert *et al.* 2006). A meta-study of passerine species also showed the earlier the males arrived the more extra-pair matings they were likely to achieve, supporting the mate opportunity hypothesis (Coppack *et al.* 2006).

### 2.1.3 Mathematical modelling is a useful tool for investigating protandry

Understanding protandry in avian migration appears to have large potential for benefit from mathematical modelling to investigate the nuances that each hypothesis would produce in male and female arrival date. Unfortunately mathematical modelling is infrequently utilised in the investigation of migratory avian species.

Protandry of arrival timings in other species has been modelled to a degree. The first general models of protandry were developed on timing of emergence in butterfly systems

(Wilklund & Fagerstrom 1977; Iwasa *et al.* 1982; Bulmer, 1983; Zonnevold & Metz, 1990), later these models were applied to arrival timings in the spawning migrations of salmon (Morbey, 2002). These models used a number of approaches including game theory, optimisation and analysis of evolutionary stable strategies (ESS). They commonly analysed only male arrival times and assumed females arrived at the same time every year. Most modelling studies make assumption that fit the mate opportunity hypothesis but some also consider the effect of survival in changing environments on males (Bulmer, 1983, Iwasa *et al.* 1983; Morbey & Ydenberg, 2001). The general results showed the importance of sex ratios and environmental constraints on male arrival; the fewer females there were the more protandry should occur because competition for females is increased and males should arrive to maximise their chances of survival against environmental constraints to mate as many times as they could.

There are very few models of protandry specifically in migratory avian species. Kokko (1999) present a game theory model that examines how condition of individuals of each sex can affect evolution of protandry on the assumption that birds of higher quality can arrive earlier and secure a better territory than other members of their sex who are of lower quality. This is effectively testing the rank advantage hypothesis. In this model Kokko assumes large birds with bright plumage arrive first because they are of better condition than their duller or smaller counterparts and this model investigates the trade off of arriving early and securing a good territory versus surviving the environmental conditions dependent on the individual's quality, indicated by body size or colouring. Her model is the first of protandry that assumes individuals of the population vary in fitness and condition. It concludes that low quality birds incur greater costs from arriving earlier than high quality birds do and should avoid early arrival as a strategy to achieve better territories.

In 2006, Kokko presented a game theory model and an agent-based model that examined the evolution of the mate opportunity and rank advantage hypothesis. Of all the protandry models this was the first integrated 'framework of protandry' that tested more than one hypothesis at a time. It was also the very first model of protandry to consider evolution of both sexes rather than only the evolution of the male. She also allows condition of individuals within the population to either be of 'high' or 'low' quality. Kokko (2006) built the mate opportunity hypothesis into their model by examining the effect of sex ratios (number of males to number of females) and through allowing males to achieve matings with females other than their mate, these are extra pair copulations (EPCs). Kokko's 2006 models do not provide support for the rank advantage hypothesis. Neither of her models from 2006 showed protandry would evolve assuming an advantage of territory acquisition alone but did show protandry would evolve when the rank advantage hypothesis was combined with the mate opportunity hypothesis. She showed both EPCs and sex ratio had a strong effect on arrival times; if one sex was scarce this caused the other sex to arrive earlier. In their model EPCs also produced protandry because it caused unmated females to become scarce and increase male-male competition.

A general review of protandry in 2012, by Morbey *et al.* considered a series of general protandry models and empirical studies and identified three factors that should influence protandry; survival rates, sex ratios and number of copulations achieved with birds other than social mates. They called for the development of theoretical understanding of how costs and benefits of late and early arrival affect protandry and particularly how the opposing forces of natural and sexual selection drive the evolution of protandry.

Other notable models consider reproductive asynchrony where male and female populations have short life spans and do not fully overlap each other. These models consider variations on three primary assumptions; an individual is not able to breed for the entire duration of their life, mating before death is not assured and populations must be tracked explicitly through the breeding phase of their lives (Calabrese et al. 2008; Lynch & Fagan, 2009; Fagan et al. 2010). These assumptions do not hold for the models presented here. First population density is not tracked so who can breed and at what stage of life is irrelevant. Second there is no explicit assumption here as to whether individuals do or do not breed however fitness for some individuals may be so low it is equivalent to them not breeding in biological terms. Thirdly although populations are tracked through their entire lives, not just their breeding phase, they are tracked through fitness and incidence of trait value, not population density of one sex relative to the other. So while these models should be noted because of the apparent similarity to the work presented here, theses similarities are quite superficial and they are not easily comparable.

### 2.1.4 The Aims of this Chapter

In this chapter I aim to use mathematical modelling to investigate the roles of natural and sexual selection as opposing forces to the evolution of protandry. I will test three of the formal hypothesis most relevant to avian species; the rank advantage, mate opportunity, susceptibly hypothesis and their interactions.

This work responds to the call of Morbey *et al.* 2012 for an ‘integrated framework’ that considers the rank advantage, the mate opportunity and the susceptibility hypothesis. This work is novel because although Kokko (2006) provided a model of mate opportunity and rank advantage it was quite complicated, particularly with the inclusion of different stochastic groups of individual quality. I believe my method is much simpler but equally as effective. In Kokko’s model she considers the effect of individual quality varying throughout the populations, here I test conditions that assume one sex can achieve generally higher probability of survival earlier in the season than the other. The Kokko (2006) model has provided very useful reflections on protandry but my model is the next step. This work is also useful because it examines the co-evolution of male and female arrival rather than just male arrival (similar to Kokko, 2006) with an integrated approach that considers the mate opportunity, the rank advantage hypothesis and the susceptibility hypothesis (novel from Kokko 2006). It is also novel because importantly the arrival date and distributions (standard deviations) of both populations are allowed to evolve.

## 2.2 Methods

I begin by presenting four models and explaining how they reflect each hypothesis and form into an integrated framework. I will then describe how I simulated long term biological evolution. Finally I will show how the models were analysed.

The first model is a control model to see how populations act under the initial environment and some basic assumptions of breeding. All subsequent models will be built on this first model. The second model considers the territory benefits early arrival brings under the rank advantage hypothesis, the third model considers the mate opportunity hypothesis and the integrated fourth model considers the interaction between the mate opportunity and the rank advantage hypothesis. To test the susceptibility hypothesis, all models were tested with environmental conditions that had equal effects on survival in both sexes, conditions that biased early survival in favour of males and conditions that biased early season survival in favour of females. Each model consists of a male and female fitness equation, $W_M$ and $W_F$ respectively. The fitness equations calculate fecundity an individual can achieve arriving on each day. Arrival date is assumed to be inherited, so birds arriving on high fitness days contribute more to the next generation than those on low fitness days and subsequently the arrival distribution of the next generation is shifted towards these days. The fitness equations are built considering behaviour at the individual level and then analysed to show how this affects the population's behaviour.

### *The arrival times of individuals within the population are normally distributed*

Arrival times in nature may be normally distributed in male and female populations of migratory birds (Hüppop & Hüppop, 2004). For all models I assume male and female distributions of arrival times throughout the population are normal functions $P_m(x)$ and $P_f(y)$ respectively (figure 2.1).

$$P_m(x) = \frac{1}{\sigma_m\sqrt{2\pi}} e^{\frac{-(x-\mu_m)^2}{2\sigma_m{}^2}}$$

(Eqn 2.1)

$$P_f(y) = \frac{1}{\sigma_f\sqrt{2\pi}} e^{\frac{-\left(y-\mu_f\right)^2}{2\sigma_f{}^2}}$$

(Eqn 2.2)

(Weinstein, 2006a)

The cumulative distributions of males, $P_m(X \leq x)$, and females, $P_f(Y \leq y)$, gives the proportion of the population who have arrived up to and including $X$ and $Y$ (figure 2.1). These are calculated using:

$$P_m(X \leq x) = \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - x}{\sqrt{2}\sigma_m}\right]$$

(Eqn 2.3)

$$P_f(Y \leq y) = \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - y}{\sqrt{2}\sigma_f}\right]$$

(Eqn 2.4)

(Weinstein, 2006b).

Where erfc$[z]$, the complementary error function, gives the area under the cumulative distribution curve (Appendix 1). This is calculated as $1 - \operatorname{erf}[z]$ where $\operatorname{erf}[z]$ is the standard error of a normal distribution function. The error functions were handled as a package supplied by MatLab. Appendix 2 shows an analysis of the properties of the probability distribution and related error function.

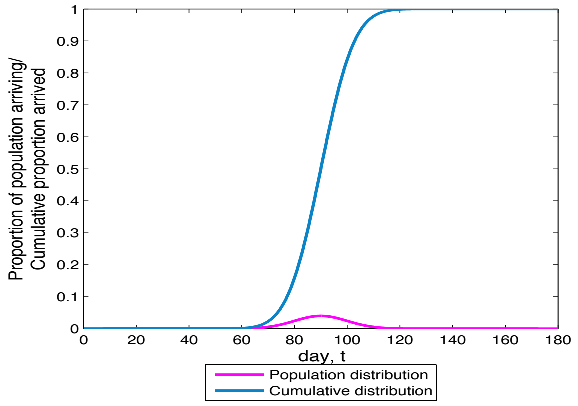

**Figure 2.1: Population distributions.**
Arrival times are normally distributed throughout the population of both sexes. The functions $P_m(x)$ and $P_f(y)$ give the proportion of the male or female population who will arrive on day $x$ or $y$ respectively. The cumulative distribution functions, $P_m(X \leq x)$ and $P_f(Y \leq y)$, show for any day the proportion of the population who have arrived up to and including those who arrive on that day.

### 2.2.1 The environment model

I begin by presenting a baseline model of a seasonal environment. As the season turns from winter to spring survival rates increase but mating and egg laying take time so a bird must trade off between its probability of survival with having time to lay and hatch eggs (Møller, 1994; Møller *et al.* 2008).

#### *Survival due to environmental conditions*

In the environment model annual temperatures from winter to spring rise are assumed to rise following a sigmoidal function, this approximates a general seasonal temperature increase for the first 6 months of the year in the Northern Hemisphere (figure 2.2). Studies show as environmental conditions improve at a breeding ground, avian survival increases so here it is assumed there is a linear relationship between temperature and survival (Ketterson & Nolan, 1976; Myers, 1981; Morbey & Ydenberg, 2001).

This model uses $s_m(x)$ and $s_f(y)$ to reflect the increasing probability of survival for an individual male or female as they arrive at the breeding ground throughout the season. Day 0 is equivalent to January 1st and day 180 equivalent to June 29th; the start and end of the breeding season (figure 2.2).

$$s_m(x) = \frac{1}{1 + e^{-a_m(x-b_m)}}$$

(Eqn 2.5)

$$s_f(y) = \frac{1}{1 + e^{-a_f(y-b_f)}}$$

(Eqn 2.6)

In the survival curves, the coefficient $a$ determines the steepness of the curve; a low $a$ indicates a shallow curve where the changeable part of the season may be many weeks long and a high $a$ indicates a steep curve where the season may change from very low probability of survival to a very high chance of survival in a matter of days (figure 2.3a).

The constant $b$ gives the midpoint of the season change, where probability of survival is 50%. A low $b$ indicates an early spring arrival, a high $b$ a late arrival (figure 2.3b). A full analysis of the effect of changing the steepness and midpoint of the curve on the length of changeable period in the season is detailed in Appendix 3.

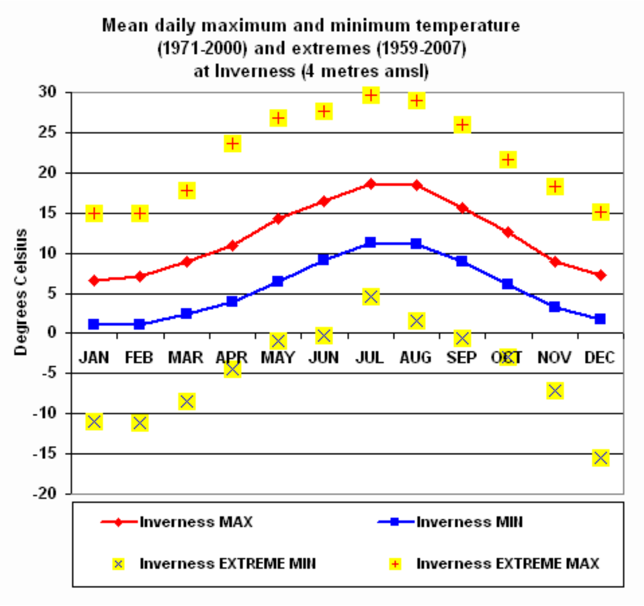

**Figure 2.2. The environmental model simulates the increasing seasonal temperatures in the Northern Hemisphere.**
In Inverness, Scotland the mean temperature rises over the first 6 months of the year in what could be approximated with a sigmoidal function (MetOffice, 2008). Here the approximation of temperature rise with a sigmoidal function has been used to describe the associated rise in survival that may be expected for the first 6 months of the year. It is assumed there is a linear relationship between temperature and survival. In the model the survival curve is approximated by, $s(t)$.

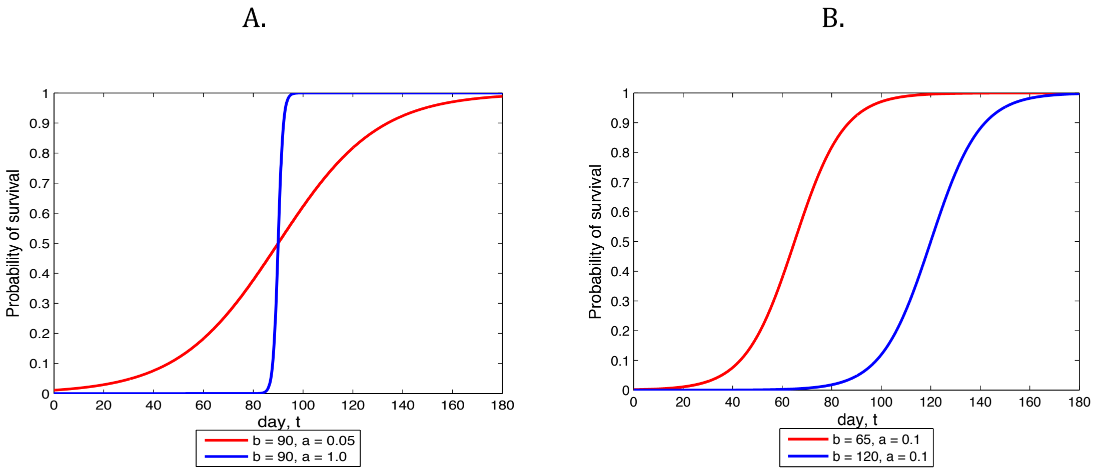

**Figure 2.3: Detailing the survival curve, $s(t)$**
Day, $t$, is used to describe any day of the season. Day $x$ is specifically male arrival date in the season and day $y$ is specifically female arrival date.

- **A. Increasing parameter $a$ makes the season change become more abrupt**. When $a$ is high the change form winter to spring is abrupt and when $a$ is low the change is gradual.
- **B. Decreasing parameter $b$ advances the arrival of spring.** Early onset of spring is given by a low $b$ value, late onset a high $b$ value.

### *Time required for reproduction*

The earlier eggs are laid in the season the more likely offspring are to survive (Møller, 1994; Møller *et al.* 2008). In this model an individual's time to rear offspring is determined by their arrival date and follows a function that decreases linearly through the season. A linear relationship is chosen for simplicity; further empirical evidence is required to increase the accuracy of this. Male and female reproductive time functions are $L(x)$ and $L(y)$ respectively where;

$$L(x) = 1 - \frac{x}{180} \tag{Eqn 2.7}$$

$$L(y) = 1 - \frac{y}{180} \tag{Eqn 2.8}$$

### *The environment model fitness equations*

The environment model consists of a male and female fitness equation built considering the individual's behaviour. The equations consider the trade off for males and females between survival and having sufficient time to raise offspring. Each equation gives the fitness, $W$, a male who arrives on day $x$, or a female who arrives on day $y$, can expect to achieve depending on the environmental conditions at that point in the season and how much time there is left in the season to lay eggs. This is, in essence, an optimisation model where the optimal arrival date is irrespective of other individuals of the same sex or opposite sex.

$$W_{M:Env} = S_m(x) \times L(x) = \frac{1}{1 + e^{-a_m(x-b_m)}} \times \left(1 - \frac{x}{180}\right)$$

(Eqn 2.9)

$$W_{F:Env} = S_f(y) \times L(y) = \frac{1}{1 + e^{-a_f(y-b_f)}} \times \left(1 - \frac{y}{180}\right)$$

(Eqn 2.10)

### 2.2.2 The rank advantage model

#### *The rank advantage hypothesis*

The rank advantage hypothesis states early arriving males gain a benefit because they can claim high quality territories easily as competition is low and many territories are available (Hasselquist 1998; Morbey & Ydenberg, 2001). Here I assume the first arriving male acquires the highest quality territory. Subsequent males acquire territories of a quality according their order of arrival in relation to other males; the first male gets the best territory, the second male gets the second best and so on until the last male gets the worst. If males seek a high quality territory to attract a mate it suggests females value high quality territories, so it may be fair to assume there is an advantage to females for arriving first out of their population so they can claim a male with a high quality territory before the other females arrive (Kokko, 2006). This is reflected in the female fitness equation.

The function used in this model for the territory quality a male achieves according to his arrival day is $Q_m(x)$ and the territory and mate a female achieves depending on her arrival date is $Q_f(y)$, where $\mu_m$ and $\mu_f$ are mean arrival dates of the male and female populations and $\sigma_m$ and $\sigma_f$ are standard deviations of the populations respectively (figure 2.4). These will play an important role in the evolution of the population and are explained further in section 2.5.5.

$$Q_m(x) = 1 - \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - x}{\sigma_m\sqrt{2}}\right]$$

(Eqn 2.11)

$$Q_f(y) = 1 - \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - y}{\sigma_f\sqrt{2}}\right]$$

(Eqn 2.12)

### *The rank advantage fitness equations*

The rank advantage model consists of the environmental model (Eqns. 5 & 6) with the territory quality function, $Q(t)$.

$$W_{M:Rank} = S_m(x) \times L(x) \times Q_m(x) = \frac{1}{1+e^{-a_m(x-b_m)}} \times \left(1-\frac{x}{180}\right) \times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - x}{\sigma_m\sqrt{2}}\right]\right)$$

(Eqn 2.13)

$$W_{F:Rank} = S_f(y) \times L(y) \times Q_f(y) = \frac{1}{1+e^{-a_f(y-b_f)}} \times \left(1-\frac{y}{180}\right) \times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - y}{\sigma_f\sqrt{2}}\right]\right)$$

(Eqn 2.14)

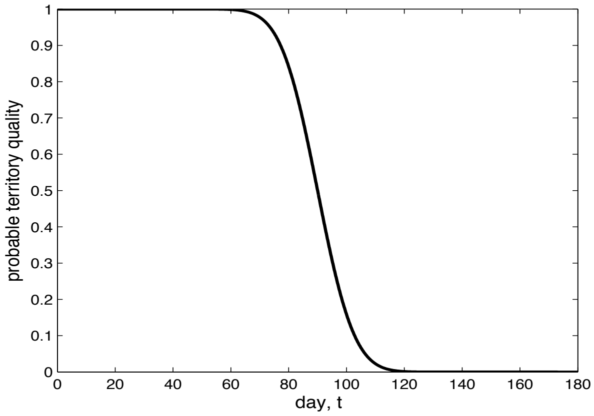

**Figure 2.4: The rank advantage hypothesis**
Territory quality decreases as competition within each sex for territories increase and territories are claimed. Territories are claimed on a first come first served basis and quality decreases in equal measures as each individual arrives. This function depends on the complementary error function of the distribution of the population. The rank advantage hypothesis applies to both sexes.

### 2.2.3 The mate opportunity hypothesis

#### *The mate opportunity hypothesis*

Most avian species are monogamous in social mating behaviour (Griffith *et al.* 2007; Akçay & Roughgarden, 2007). The mate opportunity hypothesis states that males benefit from early arrival because it increases the number of females they will encounter and thus increases his opportunities of siring more young through EPCs with females other than his monogamous partner (Huyavert *et al.* 2006). If a male arrives late, after many females have already arrived, mated and settled, the hypothesis states he has less opportunities to increase his fitness through multiple matings because he has less time to encounter females and females that have already arrived are potentially less receptive to his advances for EPCs (Morbey & Ydenberg 2001). This is illustrated in figure 2.5a and 2.5b.

In this model, male opportunity to mate is calculated using $B_m(x)$ and depends on mean female arrival and population distribution (figure 2.5c).

$$B_m(x) = 1 - \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - x}{\sigma_f\sqrt{2}}\right]$$

(Eqn 2.15)

The effect of the mate opportunity hypothesis on female birds is not fully understood and the effect of EPCs on female fitness is controversial. Some theoretical works suggest that EPCs benefit females because it provides benefit to the female through increased genetic quality of her offspring or provides her with offspring even if her mate turns out to be infertile (Griffith *et al.* 2007). A meta-analysis by Akçay & Roughgarden (2007) however concluded examples of species that gained genetic benefits from EPCs were few and showed inconsistent patterns between closely related species. Many existing studies of EPCs indicate it is the male not the female who seeks the extra matings and show EPCs are often associated with decreased male investment in parental care, so it appears likely that

EPCs are costly to female birds and may even be an example of sexual conflict (Westneat & Stewart, 2003; Arnqvist & Rowe, 2005; Akçay & Roughgarden, 2007). Furthermore there is evidence to show in many monogamous species if a male is uncertain if the brood his mate produces is his he may abandon the female and the brood (Mauck *et al.* 1999; Huyavert *et al.* 2006).

Early arrival in socially monogamous females has been empirically found to increase the probability of her having fewer young sired through EPCs (Møller *et al.* 2008). Considering these studies this model will assume early arrival is costly to female birds under the mate opportunity hypothesis because of risk of costs of EPCs. The function $B_f(y)$ shows how female risk of EPCs decreases the later she arrives depending on mean male arrival date and population distribution (figure 2.4c).

$$B_f(y) = \frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - y}{\sigma_m\sqrt{2}}\right]$$

(Eqn 2.16)

This assumption is reversed in appendix 4.

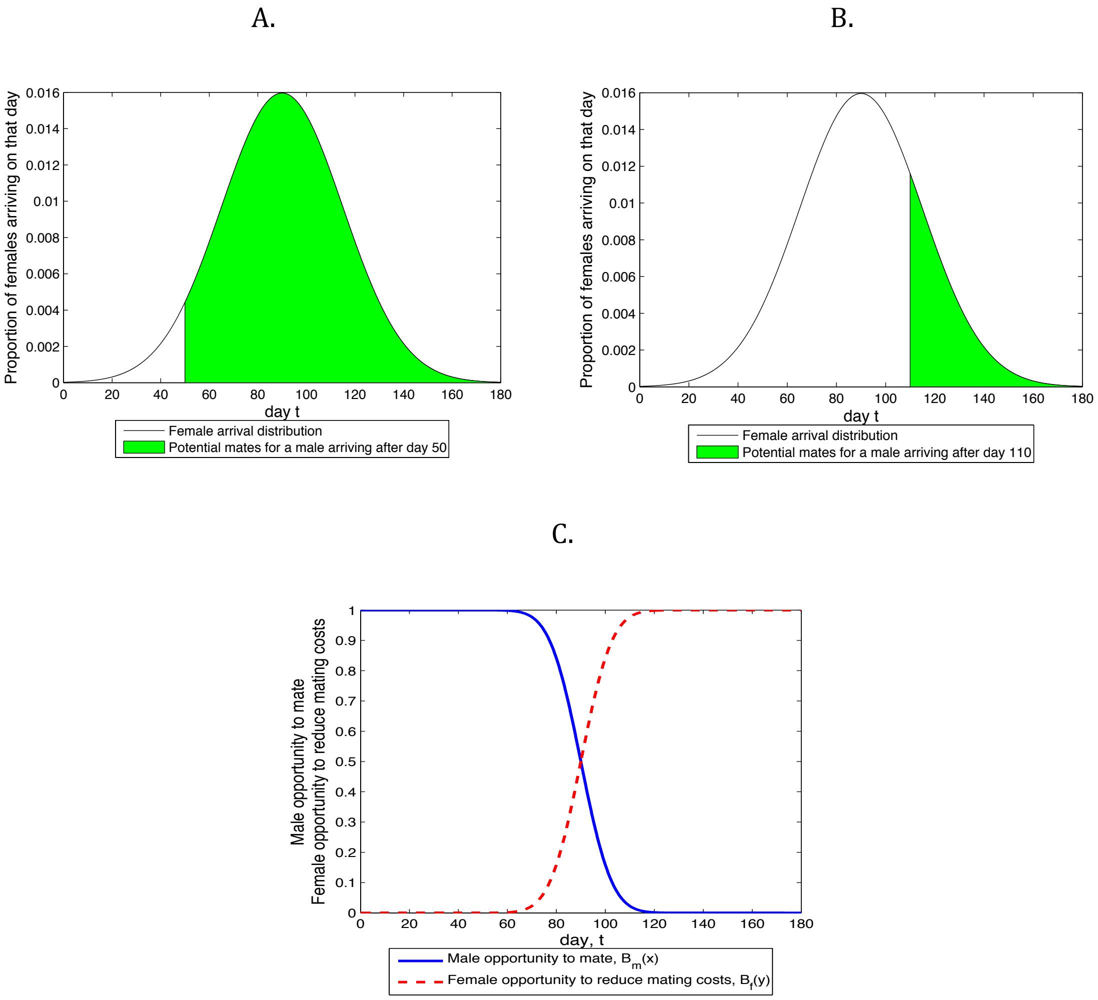

**Figure 2.5: The mate opportunity hypothesis**

- **C. Early arriving males can mate with many females**. A male may mate easily with all females who arrive after him. The earlier he arrives the more opportunities he has to mate. In all plots $t$ is Julian calendar day.
- **D. Late arriving males mate with few females.** A male who arrives late sees fewer mate opportunities as he may only attempt to mate with females who arrive after him.
- **E. Male opportunity to mate decreases through the season, female safety from EPCs increases through the season.** Opportunity to mate is high the earlier a male arrives because he is exposed to more females. The midpoint of this function depends on mean female arrival and the steepness depends on the standard deviation of the female population. Females avoid risks and costs of extra-pair or multiple matings by arriving later in the season.

### *The mate opportunity fitness equations*

The full model of the mate opportunity hypothesis builds on the environmental model (Eqns. 2.9 & 2.10) and adds the assumptions that males receive an advantage of early arrival due to increased opportunities for multiple matings or to acquire extra-pair-matings and females receive a disadvantage of early arrival because EPCs are costly to females. The male fitness is related to the female arrival and vice versa; this is supported by empirical evidence that suggests the fitness of an individual depends on his arrival date and his partner's arrival date (Møller *et al.* 2008).

$$W_{M:MateOp} = s_m(x) \times L(x) \times B_m(x) = \frac{1}{1+e^{-a_m(x-b_m)}} \times \left(1-\frac{x}{180}\right) \times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - x}{\sigma_f\sqrt{2}}\right]\right)$$

(Eqn 2.17)

$$W_{F:MateOp} = s_f(y) \times L(y) \times B_f(y) = \frac{1}{1+e^{-a_f(x-b_f)}} \times \left(1-\frac{y}{180}\right) \times \left(\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - y}{\sigma_m\sqrt{2}}\right]\right)$$

(Eqn 2.18)

### 2.2.4 The integrated model

#### *The hypothesis*

The integrated model combines the rank advantage and mate opportunity model. The model considers species where early arrival gives a territory advantage to early arrival in both sexes, an advantage through increased opportunity to mate in males and a disadvantage through increased risk of EPCs to the females.

#### *The integrated model fitness equations*

$$W_{M:Int} = S_m(x)\times Q_m(x)\times B_m(x)\times L(x)$$

$$= \frac{1}{1+e^{-a_m(x-b_m)}} \times \left(1-\frac{x}{180}\right) \times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - x}{\sigma_m\sqrt{2}}\right]\right)$$

$$\times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - x}{\sigma_f\sqrt{2}}\right]\right)$$

(Eqn 2.19)

$$W_{F:Int} = S_f(y)\times Q_f(y)\times B_f(y)\times L(y)$$

$$= \frac{1}{1+e^{-a_f(x-b_f)}} \times \left(1-\frac{y}{180}\right) \times \left(1-\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_f - y}{\sigma_f\sqrt{2}}\right]\right) \times \left(\frac{1}{2}\operatorname{erfc}\left[\frac{\mu_m - y}{\sigma_m\sqrt{2}}\right]\right)$$

(Eqn 2.20)

### 2.2.5 Modelling the evolution of arrival time

I have presented four models that detail how male and female fitness change under different hypothesis. I will now describe how fitness equations written for the individual could show the dynamics of the population as a whole and how the mean arrival date and standard deviations of the populations were allowed to evolve through time.

Depending on which model is used, the fitness an individual achieves is dictated by the day in the season it arrives, when it arrives in relation to the rest of its sex, when it arrives in relation to the opposite sex or any combination of these. Other factors that affect an individual's fitness in all models are the environmental conditions at the breeding ground on the day it arrives and how much time it has left in the season for rearing offspring.

#### *The evolution of the mean arrival date*

The mean arrival date of the $n^{\mathrm{th}}$ generation depends on the fitness of the $n-1^{\mathrm{th}}$ generation. Fitness of any generation is determined by its fitness equation, $W_i$. The slope of the fitness equation at the mean arrival date of a population is indicative of the entire population's fitness. If the fitness gradient at the mean arrival of the $n-1^{\mathrm{th}}$ generation is negative then the $n^{\mathrm{th}}$ generation gains fitness by evolving to arrive one day earlier in the season. If the gradient is positive the $n^{\mathrm{th}}$ generation would gain fitness by arriving one day later and if the gradient is zero the $n-1^{\mathrm{th}}$ generation is at a local fitness maxima for mean arrival date and the $n^{\mathrm{th}}$ generation should stay there too (figure 2.6a). Mean arrival evolves in time steps of a single day; this is to avoid fractions of days in the final output.

To state this mathematically I use the canonical equation, a standard method from adaptive dynamics of evolving traits over long time scales such as generations (Abrams, 2001; Leimar, 2009; Dieckmann & Law, 1996). Here, the canonical equation applied to a general fitness equation, $W_i$, where $i$ denotes the male or female equation accordingly, gives changes in fitness by arrival date, $t$. Note $t = x$ for male arrival and $t = y$ for female arrival.

$$\mu_i(n+1) = \mu_i(n)\, r v^2 N\, \left.\frac{\partial W_i}{\partial t}\right|_{t=\mu_i}$$

(Eqn 2.21)

Where the arguments in brackets are generation number, $n$. The canonical equation includes the rate random mutations occur in the population, $r$, the population size, $N$, and the genetic variance, $v^2$. The genetic variance is a quantitative measure of a population's scope for evolution of its arrival dates. These parameters must all be positive and real so can be grouped into a single coefficient, $\vartheta$, which in biological terms gives an estimate of how fast mutations can occur and how large they can be (Dieckman & Law, 1996; Gavrilets *et al.*, 2001; Rowe *et al.* 2005; Hoyle & Gilburn, 2010). The coefficient, $\vartheta$, is important if you want to know how long evolution will take and unimportant if you want to know where evolution will go. To reflect this, in this chapter, $\vartheta = 1$ for all equations.

$$\underbrace{\mu_i(n+1) - \mu_i(n)}_{\substack{Change\ in\ mean\ arrival\ date \\ over\ the\ generations}} = \underbrace{\vartheta}_{Speed\ of\ evolution} \underbrace{\left.\frac{\partial W_i}{\partial t}\right|_{t=\mu_i}}_{\substack{The\ fitness\ gradient \\ of\ arrival\ day\ t}}$$

(Eqn 2.22)

In summary, if the $n-1$th generation has:

| | |
|---|---|
| $\left.\frac{\partial W_i}{\partial t}\right\|_{t=\mu_i} > 0$ | the $n$th generation should evolve a mean arrival date later in the season |
| $\left.\frac{\partial W_i}{\partial t}\right\|_{t=\mu_i} = 0$ | the $n$th generation should not change its arrival date because the population has reached a local fitness maxima |
| $\left.\frac{\partial W_i}{\partial t}\right\|_{t=\mu_i} < 0$ | the $n$th generation should evolve to have a mean arrival date earlier in the season |

The partial differential equations, $\left.\frac{\partial W_i}{\partial t}\right|_{t=\mu_i}$, give the derivative with respect to arrival date evaluated at the mean, it is the fitness gradient at the mean. These equations are detailed in appendix 5.

Applied to the models presented here, the mathematical description of the between-generation changes in mean population arrival date is given by:

$$\mu_i(n) = \mu_i(n-1) + 1 \times sign\left(\frac{\partial W_i(n-1)}{\partial t}\right)$$

(Eqn 2.23)

Similar methods are used in the 'co-evolutionary stable community model' presented by Taper & Case (1992) however they consider the population size more than the work presented here does and this could be a potential avenue for future work studying the evolution of avian protandry.

### *The evolution of the population distribution*

A large novelty of this work is the population distributions evolve as well as the mean arrival date. This appears to be the first avian protandry model to do this; some previous protandry models have looked at mean arrival dates but all assumed population distribution is constant.

To allow the population distribution to evolve, the fitness curve, $W_i$, is standardised and evaluated for its width via its standard deviation at the $n-1$th generation. This is compared to the standard deviation of the population distribution of the generation. If the population distribution of the $n-1$th generation is wider than the fitness curve then the $n$th generation will evolve to be 0.1 standard deviations narrower, if is narrower then the $n$th generation will evolve to be 0.1 standard deviations wider (figure 2.6b). The value of 0.1 was chosen to allow the standard deviation to evolve yet remain relatively in line with real examples of distributions of arrival times (Hüppop & Hüppop, 2004). Evolution of the standard deviation of arrival dates allows all individuals of the population to try to maximise their fitness, not just those who arrive on the mean arrival date.

The fitness curve, $W_i$, is first standardised to give $\widehat{W}_i$. Standardised, the area under $\widehat{W}_i$ is equal to one, similar to the population distribution curve it is to be compared with:

$$\widehat{W}_i = \frac{W_i}{\sum_t W_i}$$

(Eqn 2.24)

The standard deviation of the standardised fitness curve is now calculated using:

$$\hat{\sigma}_i(n-1) = \sqrt{\sum_t \widehat{W}_i(n-1)t - \mu_i{}^2(n-1)}$$

(Eqn 2.25)

Then the standardised fitness curve and the population distribution curve of generation $n-1$ are compared to calculate the standard deviation of the population distribution of generation $n$:

$$\sigma_i(n) = \sigma_i(n-1) + \ 0.1 \times sign(\hat{\sigma}_i(n-1) - \sigma_i(n-1))$$

(Eqn 2.26)

Similar methods are presented in Slatkin & Lande (1976).

### *Notes on the assumptions of evolution*

The models assume that each function, $S(x)$, $S(y)$, $L(x)$, $L(y)$, $Q(x)$, $Q(y)$, $B(x)$ and $B(y)$, exerts directional selection on the population trait, either male arrival date distribution, $P_m(x)$, or female arrival distribution, $P_f(y)$,and it assumes that the populations always evolve to an equilibrium. Models are allowed to run to equilibrium to fully understand the effect of each parameter independent of time.

The models all tend to a single equilibrium; while further equilibrium points may exist they are out with the biologically relevant range ($T[0,180]$). The work here assumes the final values at equilibrium are always a local maxima point, where population fitness is maximised; while it is possible they could be a minima, where population fitness is in fact at its minimum, the use of the canonical equation makes this highly unlikely (Eqn 2.22) for two reasons. First, the canonical equation always moves the population away from a minima; when the fitness gradient is negative the mean arrival date shifts earlier in the season and when the fitness gradient is positive it shifts later in the season. This leads to the second reason achievement of a minima is unlikely; the only way a minima can be achieved is if the initial conditions are exactly that of the minima equilibrium value. Under these conditions the fitness gradient would equal zero and the population would be 'trapped' at its fitness minima. To avoid this every iteration of model was reviewed, if the plot of $T$ and $x$ over evolutionary time showed no deviation from the initial value it was to be run again with slight deviations in initial conditions to establish if it had not accidentally reached a minima; in practice this method was never required. It is however possible that the model could tend to a local maxima rather than a global one; to check this was not the case fitness functions for each final generation were examined, these are illustrated in appendix 4.

The models in this chapter assume the strength of selection is constant; only the sign of the fitness gradient affects the evolution of the population. Regardless of the value of the gradient of the fitness equation at the mean arrival date the mean arrival date of the $n^{\text{th}}$ generation will only ever be $\pm 1$ day and the distribution will be $\pm 0.1$ standard deviations smaller than the $n-1^{\text{th}}$. The use of the sign of the fitness gradient alone is appropriate because the model is run until a fitness maxima is achieved, to the nearest integer solution. This assumption echoes assumptions of Taper & Case (1992) who although show a continuous model, whereas this work is discrete with a fresh evaluation of fitness and distribution at each generation, still assume that the time taken to reach evolutionary conclusions is largely irrelevant until the direction of the evolution is established.

In her 1999 paper, Kokko uses game theory methods to explore competition in cost benefit trade-offs between small numbers of individual birds. She uses a Stackleberg game structure. This means each player, bird, takes turns to choose an arrival date and the following player can react to this (Osborne & Rubinstein, 1994). This is very different to the methods presented here. These methods are inappropriate for the work here to use because if combined with the extra factors included here would have made the models unnecessarily complicated. In her 2006 paper, Kokko presents first a model where there exist discrete groups of quality for individuals, overall population fitness is determined by summing the number of birds of each quality group multiplied by the fitness achievable in each quality group. Once actual population fitness is calculated, it is numerically analysed using a mean arrival date different by 0.001 days, if the test population fitness with a mean arrival date 0.001 days later than the actual mean arrival date produces a larger fitness then the subsequent generation will evolve a later arrival date. The work presented here uses a similar approach to the methods of Kokko (2006). The second model Kokko (2006) presents is individual based; this model tracks the numbers of individual males and females in real time. The differences between all these methods matter to a degree and useful is to use many methods on the same problem and compare the outcomes; where possible this has been done here and comparisons between the results here and the results of the other models of avian protandry have been detailed in the discussion.

### *Computer programming was used to simulate evolution*

The programming package, MatLab, was used to build a program to run evaluations of the partial differential equations for each model. This allowed for evolution through time of the male and female populations incorporating the fitness gradient to evolve the mean arrival date and evaluation of the width of the fitness curve to evolve population distributions. For illustration the program for the environment model is included in appendix 6.

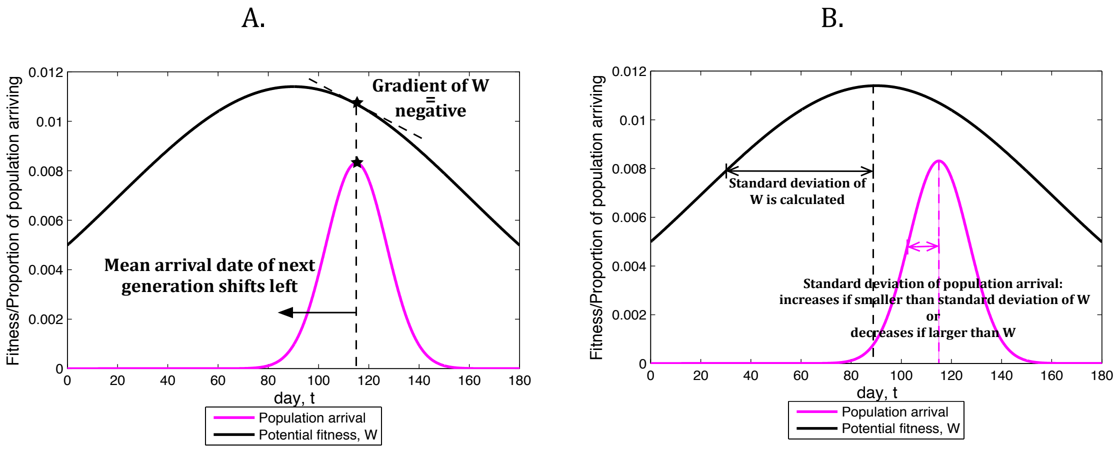

**Figure 2.6: Mean arrival date and standard deviation of the populations may evolve.**

- **A. Evolution of the mean arrival date are calculated using the fitness gradient of $W$.** The mean arrival date of the nth generation depends on the gradient of the fitness curve, at the mean arrival date of the $n - 1^{\text{th}}$ generation. If the gradient of the $n - 1^{\text{th}}$ generation is negative the mean arrival date of the $n^{\text{th}}$ generation is shifted 1 day earlier, if positive it is shifted 1 day later. In both plots $t$ is Julian calendar day.
- **B. Manipulating standard deviation.** If the standard deviation of the $n - 1^{\text{th}}$ generation is wider than the standardized width of the fitness curve then the width of the nth generation population distribution evolves to be 0.1 standard deviations smaller than the previous generation, if the $n - 1^{\text{th}}$ generation distribution is narrower than the fitness curve the nth generation evolves to be 0.1 standard deviations larger.

### 2.2.6 Analysing the Models

Although simple in structure and parameter number these models are still too difficult to solve analytically through normal methods due to the normal distribution functions used to describe the population dynamics and also due to the four evolving variables, $\mu_m$, $\mu_f$, $\sigma_m$ and $\sigma_f$. Every time a model is used these evolving variables must first be set with an initial value, if there are multiple equilibrium points the initial value of these parameters determine which equilibrium the final values will evolve towards. Solving for a full analytical solution involves determining where each equilibrium point lies and whether it is stable or unstable; whether the evolving parameters are attracted towards it or repelled from it. For these models this would have to be calculated in four dimensions and would be as difficult to display as it would be to calculate.

#### *Models were tested by hand to find numerical solutions*

Each model has three different versions that are used to account for the susceptibility hypothesis; equal survival between the sexes, male biased survival and female biased survival. First the environment model was analysed for each survival version to locate biologically realistic equilibrium that fell for $t$ within [0,180] days. One was found for the model with equal survival at $\mu_m = \mu_f = 109$, and $\sigma_m = \sigma_f = 26.2$, another for the male biased environment model at $\mu_m = 65$, $\mu_{f=}145$, $\sigma_m = 18.4$ and $\sigma_f = 28.4$ and a third for the female biased model at $\mu_m = 145$, $\mu_{f=}65$, $\sigma_m = 28.4$ and $\sigma_f = 18.4$. These were confirmed as equilibrium points because if the values of $\mu_m$, $\mu_f$, $\sigma_m$ and $\sigma_f$ for each model version were set at the respective equilibrium values, the final value the model populations evolved to was exactly the same. The points were then found to be stable because when the model was tested with a range of values around the equilibrium points they always evolved to the same equilibrium point.

After these initial equilibrium points were determined from the environment model they were set as initial conditions for each of the rank advantage, mate opportunity and integrated models for equal, male biased and female biased survival respectively. This allowed the models to be tested over ranges of $a_m$, $a_f$, $b_m$ and $b_f$ where it was known that a biologically relevant equilibrium existed. Each survival version of the model was tested over a different range of parameters; the equal survival models were tested with $a_m = a_f$ and $b_m = b_f$, the male biased survival models where tested with combinations of $a_m > a_f$ and $b_m < b_f$ and the female biased survival models were tested with combinations of $a_m < a_f$ and $b_m > b_f$. To begin, two sets of example parameters were chosen; the first set used $a_m$, $a_f$, $b_m$ and $b_f$ values that produced a very large, extreme difference in male and female survival curves for the male biased and female biased model versions and the second set used $a_m$, $a_f$, $b_m$ and $b_f$ values that depicted a more biologically relevant survival scenario. The extreme set of parameters was used to find obvious behaviours of the model, the second set was used to then confirm findings of the behaviours and then further values of $a_m$, $a_f$, $b_m$ and $b_f$ were used to refine the conclusions and look out for unexpected sensitivities of the model. The parameter values and resulting survival curves for equal, male biased and female biased survival at extreme and more biologically relevant parameters are detailed in figure 2.7. Although this does not constitute a full mathematical analysis of the Cartesian space the model exists in, it does provide a good understanding of the biologically relevant parameter space and allows conclusions about parameter effects to be drawn.

### *Results are displayed as a snapshot of the general patterns each model shows*

To display the results a snapshot of each model is shown (figures 2.9 - 2.12) showing the final evolutionary values of $\mu_m$, $\mu_f$, $\sigma_m$ and $\sigma_f$ for each model using the biologically relevant set of parameter values. Alongside the snapshot of results is summarised the general patterns each model shows over the full parameter analysis. Please note extreme care was taken with this sensitivity analysis of the models and to check the biologically relevant parameters and the resulting snapshots of final evolution population distributions are actually representative of the each model. Each snapshot of the rank advantage, mate opportunity and integrated model is displayed alongside the equivalent snapshot of the environment model for comparison of results between models.

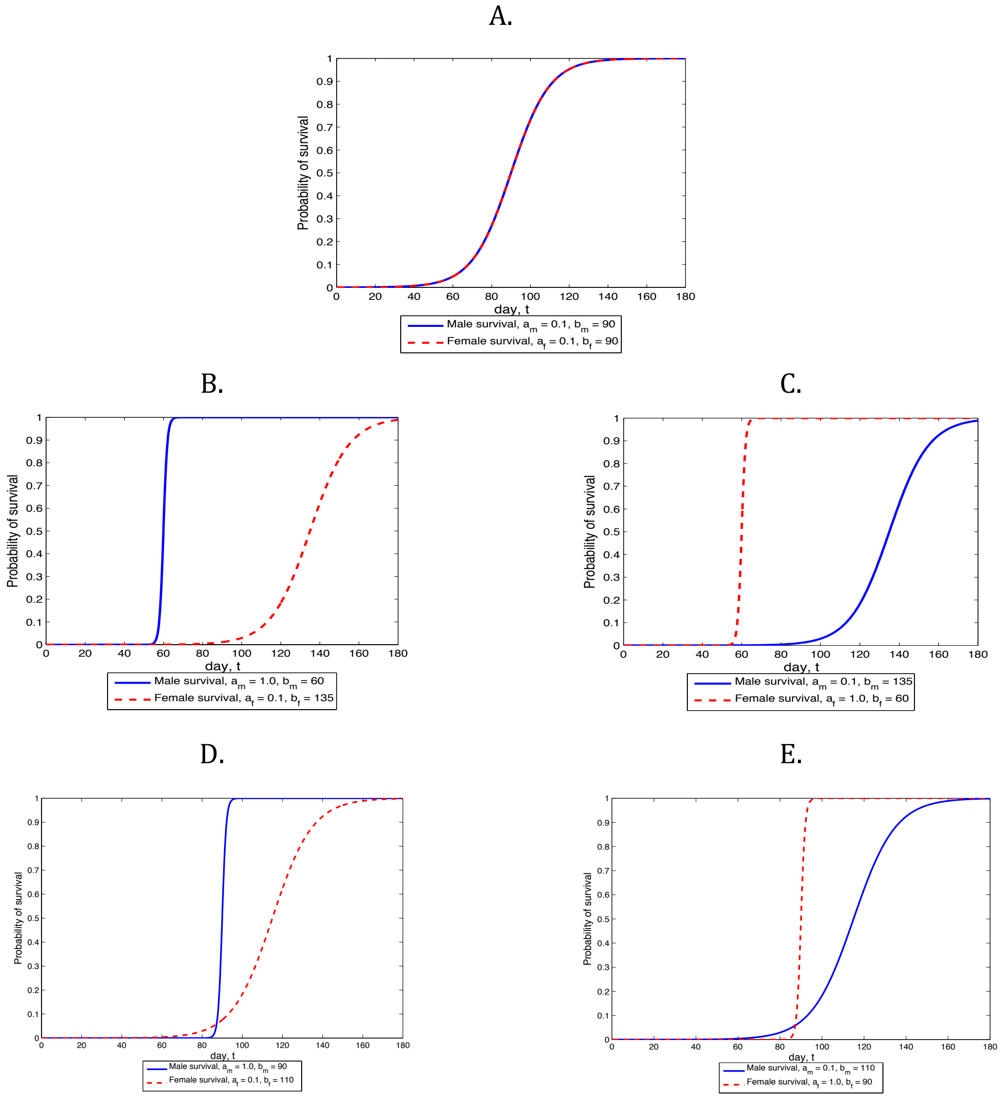

**Figure 2.7: Models were tested under different sets of survival parameters.**

- **A. Equal conditions of survival.** Both $a$ and $b$ parameters are equal for males and females and set at an intermediate value. In all plots $t$ is Julian calendar day.
- **B. Extreme parameter set: Male biased survival.** Males have a steep survival curve and females have a shallower survival curve. The difference between midpoints of survival curves is 75 days.
- **C. Extreme parameter set: Female biased survival.** Females have a steep survival curve and males have a shallower survival curve. The difference between midpoints of survival curves is 75 days.
- **D. More biologically relevant parameter set: Male biased survival.** Males have a steep survival curve and females have a shallower survival curve. The difference between midpoints of survival curves is 20 days.
- **E. More biologically relevant parameter set: Female biased survival.** Females have a steep survival curve, males have a shallower survival curve. The difference between midpoints of survival curves is 20 days.

## 2.3 Results

### 2.3.1 A sensitivity analysis of parameters $a$ and $b$

The environmental model is used to examine the effects of changing environmental survival and act as a control for the other models to be compared to. First it was used to investigate how changing parameters of the survival function, $s(t)$, would affect the population's arrival. To do this male and female survival were assumed to be equal ($a_m = a_f = a,\ b_m = b_f = b$). As $a$ increases the change from winter to spring happens faster, this results in populations evolving to arrive earlier and over a narrower range (figure 2.8a). As $b$ decreases spring arrival advances earlier in the season, this causes populations to arrive earlier and with a wider distribution (figure 2.8b). The general effect of $a$ and $b$ is consistent for all models.

The fitness curve of the final male and female generation for every model and combination is illustrated in appendix 4.

### 2.3.2 Results of the environment model

The environment model shows when conditions exert the same survival rates on the male population as the female population the sexes will evolve to arrive on the same day and the degree of protandry will be zero (figure 2.9a).

If survival is male biased protandry occurs with the male population arriving with a wider distribution than the female population (figure 2.9b). It is noteworthy that the fitness curve of the final generation of males however shows a steep step which runs through the expected middle of the population distribution curve the model predicts (figure 7.3b). This indicates that a large number of individual males, nearly half the population achieve a fitness of almost zero. In reality this would not happen as these individual would not survive. This illustrates a limitation of the model in its inability to evolve the shape of the population distribution to align with the fitness curve best.

If conditions are female biased arrival curves are reversed. When females arrive before males this is termed protogyny (figure 2.9c). Female fitness curve shows a similar step in fitness curve as the reverse of male biased survival (figure 7.3c).

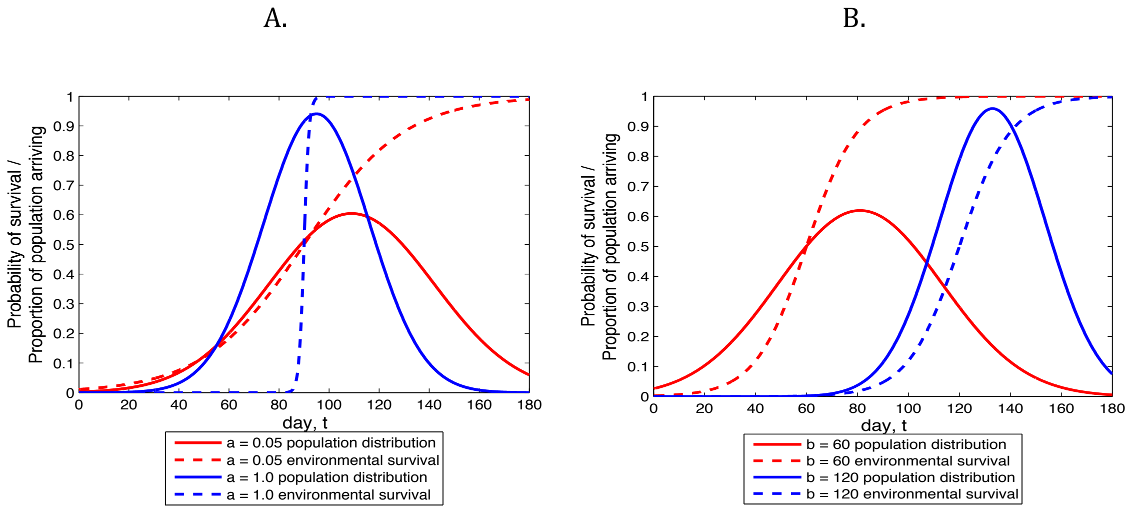

**Figure 2.8: The general effect of changing survival function parameters *a* and *b***

A. **The effect on population arrival of increasing *a*, the slope of the survival curve, in the environmental control model.** As *a* increases and season switch occurs faster both sexes evolve to arrive earlier and with a narrower distribution. In both plots *t* is Julian calendar day.

B. **The effect on population arrival of increasing *b*, the midpoint of the survival curve simulating later arrival of spring, in the environmental control model.** As the arrival of spring becomes earlier both sexes evolve to arrive earlier.

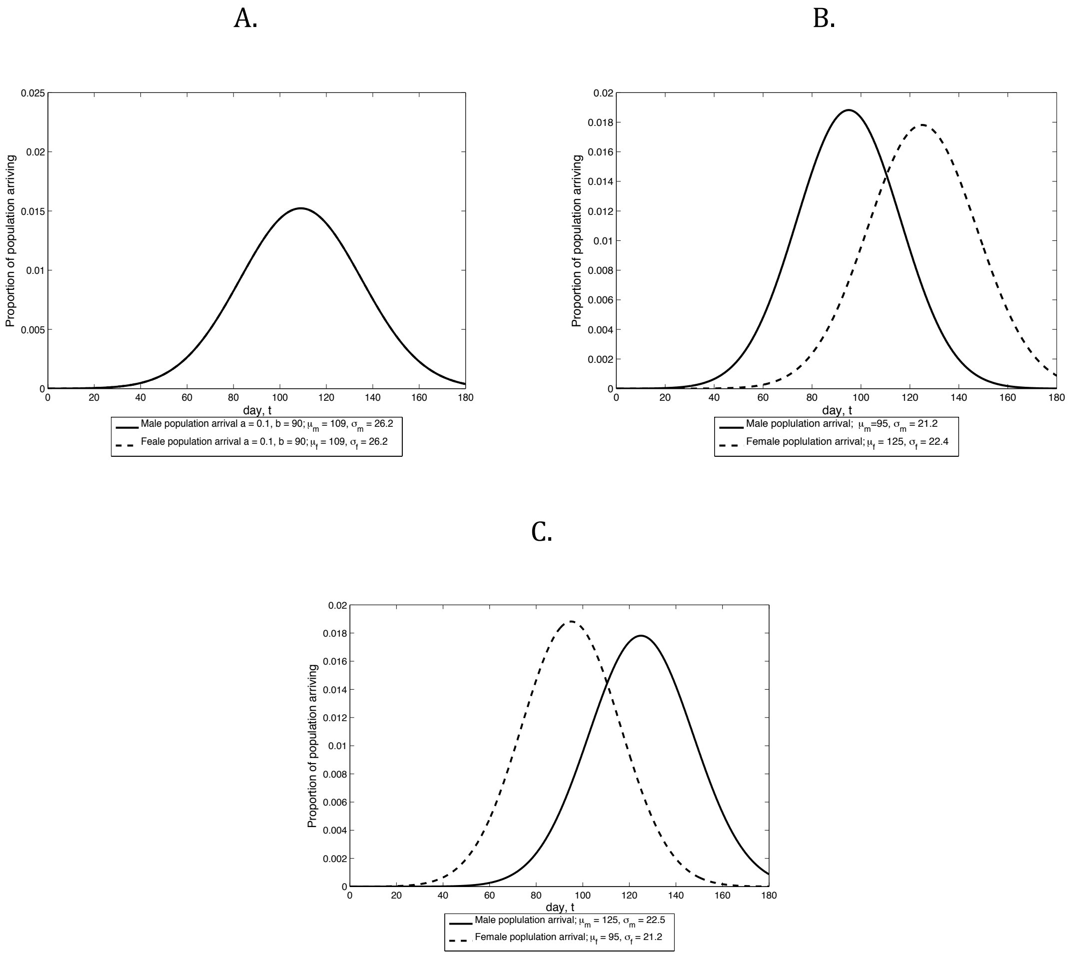

**Figure 2.9: A snap-shot of results of the environmental model**

A. **Equal environmental survival result in equal male and female arrival distributions.** When conditions are equal for both sexes and females, $a_m = a_f = 0.1, b_m = b_f = 90$, evolve to arrive on the same day with equal distributions. Final values of male and female mean arrival and standard distributions are detailed in the legend. In all plots $t$ is Julian calendar day.
B. **Male biased survival results in protandry.** When conditions are biased towards male survival, $a_m = 1.0, a_f = 0.1, b_m = 90, b_f = 110$, male mean arrival date is earlier than the female's and male distribution is narrower.
C. **Female biased survival results in protogyny.** Female mean arrival date is earlier than the male's and female distribution is narrower when survival is female biased, $a_m = 0.1, a_f = 1.0, b_m = 110, b_f = 90$. Population distributions for female biased survival are the reverse of those that evolved under male biased survival.

### 2.3.3 Results of the rank advantage model (same sex competition)

When survival is equal neither protandry nor protogyny evolves, male and female populations arrive simultaneously with equal mean arrival dates and equal distribution. Arrival distributions under the rank advantage model are earlier and narrower than under the environment model (figure 2.10a).

When survival is male biased then protandry will evolve, the more heavily male biased survival becomes the larger the degree of protandry that evolves. The difference between male and female mean arrivals under the rank advantage model in this snap-shot is decreased by 12 days compared to the environment model. The populations under the rank advantage model show almost no overlap in arrival times; all of the males have arrived before the first females arrive. The mean arrival of the male distribution under the rank advantage model is 4 days earlier than under the environment model and the distribution is considerably narrower ($\sigma_m$ decreases from 28.4 to 1.8). The female mean arrival is 16 days earlier than the environmental model and the distribution is slightly narrower with $\sigma_f$ decreasing from 18.4 to 16.8 (figure 2.10b). The male population distribution closely mirrors the male fitness curve (figure 7.4b). The female population distribution width mirrors that of the fitness curve distribution width but females achieve a relatively higher fitness than their population distribution curve might suggest (figure 7.4b).

When survival is female biased protogyny evolves and arrival distributions and final fitness curves are the exact reverse of those that occurred under male biased survival (figure 2.10c, figure 7.4c).

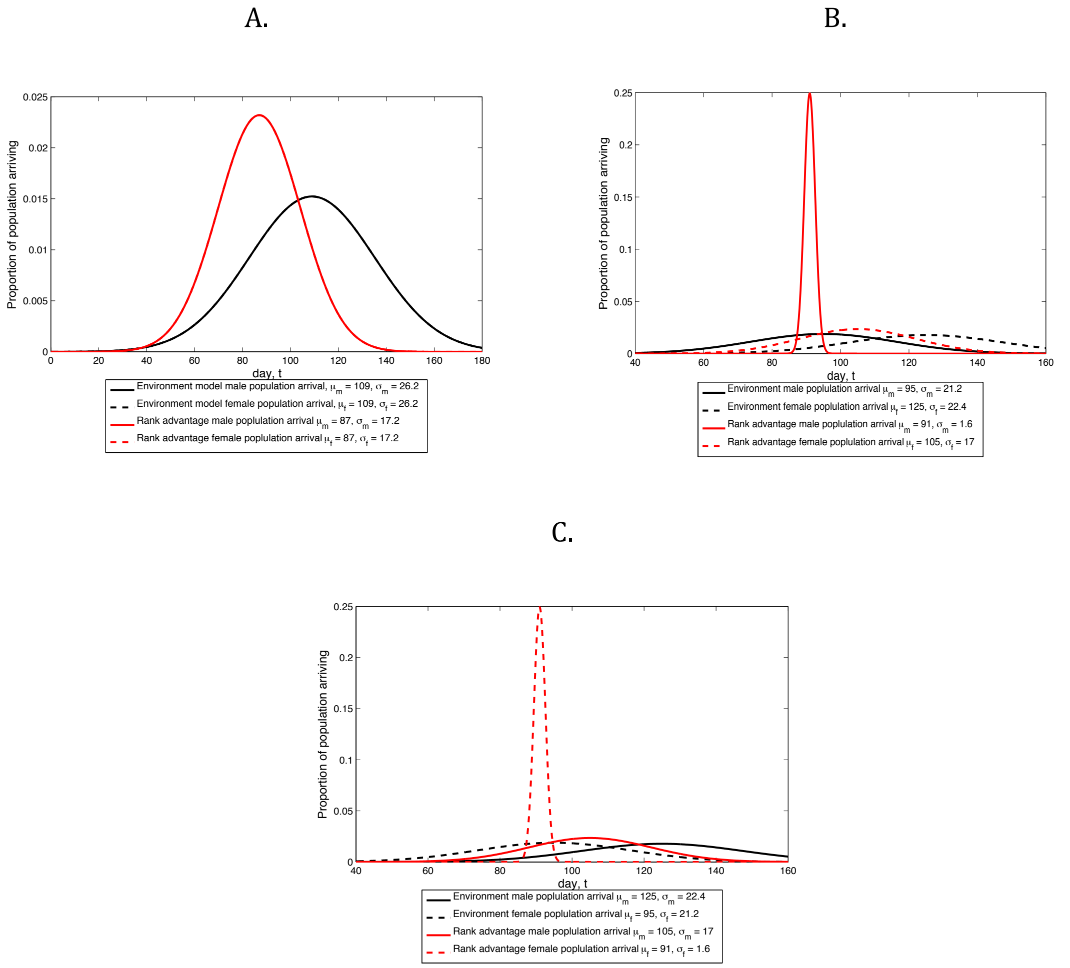

**Figure 2.10: A snap-shot of results of the rank advantage model compared to the environment model.**

A. **Equal environmental survival results in equal male and female arrival distributions.** With no survival differences, $a_m = a_f = 0.1, b_m = b_f = 90$, both sexes arrive with equal distributions. The populations arrive earlier and with a narrower distribution than the environment model. In all plots $t$ is Julian calendar day.

B. **Male biased survival results in protandry.** Protandry persists when survival is male biased, $a_m = 1.0, a_f = 0.1, b_m = 90, b_f = 110$. Male arrival distribution is much narrower than the environment model and mean arrival is earlier for both male and female populations than the environment model.

C. **Female biased survival results in protogyny.** When survival is female biased, $a_m = 0.1, a_f = 1.0, b_m = 110, b_f = 90$, a large degree of protogyny is evident and distributions are the exact reverse of those seen under male biased survival.

### 2.3.4 Results of the mate opportunity model (between sex competition)

When there is no survival bias the mate opportunity model shows the sexes will evolve to arrive on the same mean date but females will have a slightly wider distribution ($\sigma_m = 19.4$, $\sigma_f = 20.8$ for the snap-shot example); the very first females will arrive slightly before the very first males but the very last males arrive before the very last females. There is no difference in mean arrival dates of both populations between the mate opportunity and environment models but both male and female distributions are slightly narrower than the environment model (figure 2.11a).

When survival is male biased then protandry will evolve; males arrive 30 days earlier than females and with a narrower distribution, similar to the pattern of arrival in the environment model with male biased survival. Degree of protandry increases as survival become more biased allowing males to survive even earlier. Both male and female populations have the same mean arrival date under the mate opportunity model as they do with the environment model with male biased survival but the mate opportunity model shows narrower distributions ($\sigma_m = 21.2$ initially then rose to 14.4 and $\sigma_f = 22.2$ initially then fell to 19.6, figure 2.11b). Male fitness shows a steep step in the curve with many individuals arriving early achieving almost zero fitness, female population distribution is early compared to the maximum point of their fitness curve (figure 7.5b).

When survival is female biased protogyny evolves under the mate opportunity model as it does under the environment model and to the same degree; females arrive 30 days before males in the snap-shot. The degree of protogyny increases the more biased survival becomes towards the females. In the mate opportunity model female arrival distribution is slightly wider than male distribution ($\sigma_m = 17.6$, $\sigma_f = 18.4$). Female mean arrival date under the mate opportunity model is the same as under the environment model but much more narrowly distributed (figure 2.11c).

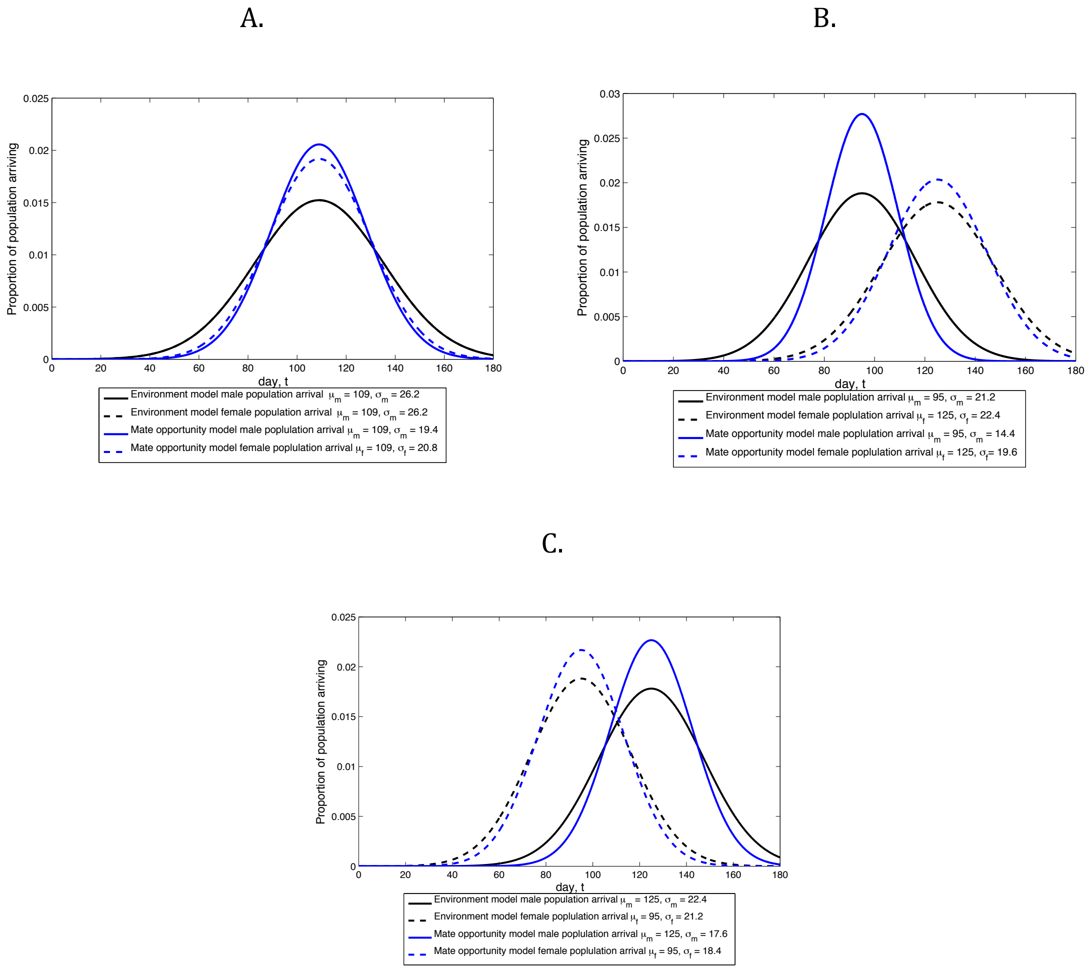

**Figure 2.11: A snap-shot of results of the mate opportunity model compared to the environment model.**

A. **Equal environmental survival results in neither true protandry nor protogyny.** With no survival bias, $a_m = a_f = 0.1, b_m = b_f = 90$, the populations evolve equal mean arrival dates but female population is slightly more widely distributed than male so the very first females arrive just before the very first males. Both population's distributions are narrower than the environmental model. In all plots $t$ is Julian calendar day.

B. **Male biased survival results in protandry.** Protandry evolves when survival is male biased, $a_m = 1.0, a_f = 0.1, b_m = 90, b_f = 110$, under the mate opportunity hypothesis. There is no increase in difference in male and female mean arrival dates from the environment model but the mate opportunity has narrower distributions, particularly the males, so there is less overlap between the sex' arrival times.

C. **Female biased survival results in protogyny.** Protogyny evolves when survival is female biased, $a_m = 0.1, a_f = 1.0, b_m = 110, b_f = 90$, under the mate opportunity hypothesis. There is no increase in difference in male and female mean arrival dates from the environment model but the mate opportunity has narrower distributions so there is less overlap between the sex' arrival times. The female biased model shows a larger reduction in female distribution width than the male biased model but a smaller reduction in male distribution width.

### 2.3.5 Results of the integrated model

When survival is equal for both sexes mean male arrival date is 2 days earlier than mean female arrival and the male population has the wider distribution; protandry evolves. These are both much earlier than the mean arrival under the environment model, the males by 28 days and the females by 26 days (figure 2.12a).

When survival is male biased protandry evolves. Both sexes arrive very early in the season and with a narrow distribution, $\sigma_m = \sigma_f = 1.4$ in the snapshot. Male arrival is 2 days before females. Male arrival is 6 days earlier under the integrated model than under the environment model and female arrival is 34 days earlier (figure 2.12b). As survival becomes more male biased male arrival evolves to be progressively earlier as female arrival evolves to be later. Female arrival distribution is markedly wider in the extreme value parameter set compared to the biologically relevant parameter set. The final distribution of the male population closely matches the final fitness curve of the male population but female distribution is much earlier than the maximum of their fitness curve (figure 7.6b).

When survival is female biased protogyny evolves; female mean arrival is 4 days earlier than male arrival and much narrower ($\sigma_m = 11.4$, $\sigma_f = 1.6$). Male mean arrival is 30 days earlier than under the environment model and female mean arrival is 34 days earlier. Distributions are dramatically reduced from the environment model to the integrated model (figure 2.12c). As survival becomes more biased towards females, female arrival evolves to become earlier and narrower and male arrival is later and wider.

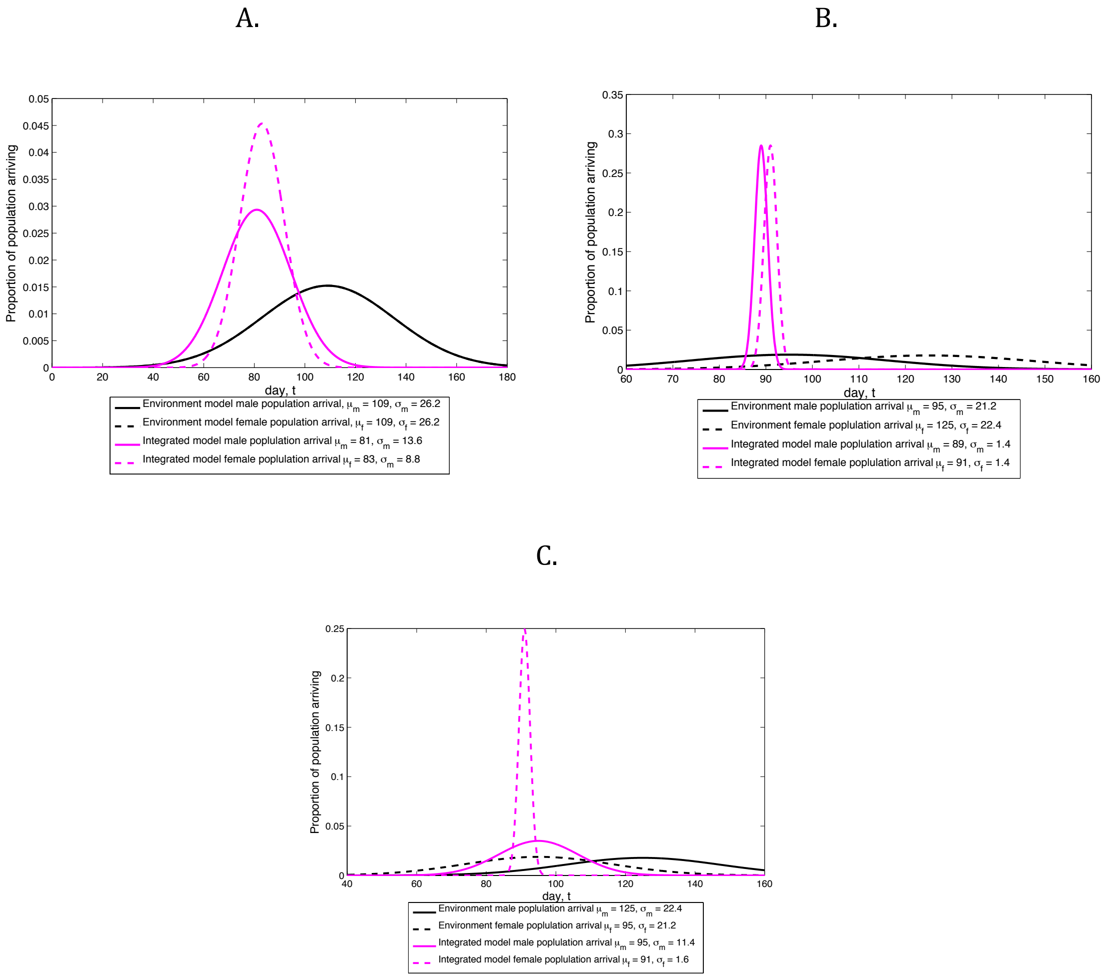

**Figure 2.12: A snap-shot of results of the integrated model compared to the environment model.**

- **A. Equal environmental survival results in protandry.** Male mean arrival date is earlier than female mean arrival date and male distribution is wider; the first males arrive before the first females and the whole population of males arrive on average earlier than females. Parameters are $a_m = a_f = 0.1, b_m = b_f = 90$. In all plots $t$ is Julian calendar day.
- **B. Male biased survival results in protandry.** Both populations evolve to arrive earlier than the environmental model and with a narrower distribution when survival is male biased, $a_m = 1.0, a_f = 0.1, b_m = 90, b_f = 110$. The distribution of both sexes is very narrow.
- **C. Female biased survival results in neither true protandry nor protogyny.** Although mean arrival dates of females are earlier than males, the male distribution is very wide such that the first arriving individuals are male. However the majority of the female population has arrived before the majority of the male population. This may be an illustration of the importance of the shape of the population distribution. Parameters are $a_m = 0.1, a_f = 1.0, b_m = 110, b_f = 90$.

## 2.4 Discussion

Four models were presented; the first an environment model of a population subject only to environmental based survival rates at a breeding ground and egg laying time limitations. The second and third models added assumptions of benefits of early arrival through the rank advantage and mate opportunity hypothesis respectively and the fourth model combined all hypotheses. Models were tested assuming equal survival between the sexes, a bias that permitted earlier male survival and a bias that permitted earlier female survival. Each model considers assumptions about both sexes and the interaction between and within sexes. Evolution is simulated through a fitness weighting of individuals with the highest reproductive output according to what day they arrive, distribution width and mean arrival date of the offspring population is shifted accordingly. Models were tested over a wide range of parameter values, formally over an extreme parameter set and a biologically relevant parameter set and informally over parameters in between, to ensure conclusions were accurate representations of the model behaviour (figure 2.7). Model behaviours are illustrated using a snapshot method where the dynamics of the evolution of the models under the biologically relevant set of parameters are displayed and used to summarise general results of each model.

Here I discuss the findings of the models, the value of each and how they relate to other theoretical and empirical studies. These models are novel because they are the first to combine the mate opportunity and rank advantage hypotheses with the susceptibility hypothesis as an integrated framework. They are also the first models of protandry in migratory birds to allow the distribution of the population as well as the mean arrival to evolve, allowing the population to evolve complex behavioural strategies.

### 2.4.1 Environment plays a key role in the evolution of protandry

The first result the models show is that the susceptibility hypothesis is likely to play an influential role in the evolution of protandry. This is demonstrated in two ways; first by the effect of the parameters $a$ and $b$ on the general arrival times and distributions (figure

2.8). Second this is demonstrated by the effect of sex differentiated effects of survival in each model, when a sex bias of environmental survival is applied the favoured sex always evolves to arrive earlier than the unfavoured sex. Individuals should arrive as early as their condition allows to maximise the time they have in the breeding season to raise offspring. In nature male biased survival is more common in birds than female biased survival (Owens & Bennet, 1995; Møller *et al.* 2004). A male survival bias could be caused by a number of factors; females often winter further from the breeding ground than males, so have a longer migratory journey which leaves them overtly vulnerable for longer and likely to arrive at the breeding ground weaker and more fatigued than those with shorter distances to fly (Smith, 1988). Differences in body size may also contribute to a male survival bias; species where female body size is smaller than the male's are likely to have male biased survival as females are more susceptible to harsh environmental effects early in the year (Morbey & Ydenberg, 2001). Other studies suggest that survival may be biased in favour of males in birds generally due to increased costs of feeding and raising offspring in the nest the females face (Owens & Bennet, 1995).

The evidence for the role of sex biased survival on protandry in the wild is mixed; studies of barn swallows and warblers have shown no association between degree of male bias in survival and degree of protandry (Francis & Cooke, 1986; Møller *et al.* 2008), yet a study of a different population of barn swallows and a study of American redstarts showed a strong association between degree of male biased survival and protandry (Møller *et al.* 2007; Reudnick *et al.* 2009). Here, the susceptibility hypothesis, as male biased survival, shows an increase in the degree of protandry under every model. This is through increasing the difference between male and female mean arrival or by decreasing the distributions of the populations to the point where population arrivals are so disconnected almost all males have arrived before the majority of the females as in the integrated model (for example figure 2.12b).

### 2.4.2 The rank advantage hypothesis alone is insufficient as an explanation for the evolution of protandry

The second result the models show is the rank advantage hypothesis alone is insufficient to cause protandry or protogyny to evolve although it can cause a general advancement of mean arrival dates. The rank advantage model snapshot with equal survival shows male and female populations arrive 22 days earlier and with a narrower distribution than the environment model. This early arrival shows the benefit of territory gained from early arrival must be worth the decreased probability of survival due to early arrival. When arrival is narrowly distributed it indicates high competition as more individuals compete each day for territories, this may reflect the value of territory to the individual because even the very last arriving individuals don't want to be too far behind the rest of the population.

Kokko's 2006 model also showed the rank advantage hypothesis be insufficient to cause protandry to evolve and the models presented here support her findings. Both the models presented here and Kokko (2006) assume that females as well as males compete for early arrival for good territories but in contrast to Kokko (2006) the models presented here do not assume that females must wait for males to arrive before they can claim a territory. Kokko (2006) also suggests that sex ratio, which they suggest could be loosely approximate to sex biased survival, is a strong driving force in the evolution of protandry or protogyny. The models presented here strongly support both these claims. This is a useful validation of each other's models because both models came to similar conclusions making different assumptions and using very different methods.

A third result the models show is that although the rank advantage hypothesis alone is insufficient to drive the evolution of protandry, when combined with the susceptibility hypothesis the rank advantage hypothesis may provide an explanation for protandry. With the susceptibility hypothesis, if survival is male biased protandry evolves and if survival is female biased protogyny evolves. As survival bias increases difference in mean arrival dates increase. Regardless of bias, the first arriving sex always arrives with a very narrow distribution in the rank advantage model, this could be a reflection of the slope of the survival curve. Environmental conditions are changing around the time in the season where the survival curve falls as the probability of survival changes from almost zero in the winter to almost one in the spring, how many days this takes depends on the slope of the survival curve (full mathematical details and explanation of the length of changing period and how this relates to the slope of the survival curve are detailed in appendix 3). The first and last arriving individuals evolve to be right on the costs limits dictated by the population's survival curve; if the first arriving individuals were to arrive even marginally earlier they would receive disproportionately large increases in costs of survival for small gains in territory. It is likely this distribution would be wider if the survival curve was slightly shallower. Last arriving individuals of the favoured sex arrive very shortly behind first arriving individuals when the survival curve is very steep and the length of time of the season change is very short because beyond the season changing period there are only small costs of survival but large benefits of territory for advancing arrival date. If the survival curve is gentler then population distributions curves are wider. This is supported separately from the sensitivity analysis of the parameters $a$ and $b$ of the survival curve; a steep curve results in an early narrow arrival distribution, a shallower curve results in a later and wider arrival distribution (figure 2.8).

However a population distributes itself, early arriving individuals incur high costs of survival but good benefits of territory and late arriving individuals incur low costs of survival but poor benefits of territory under the rank advantage model. The width of the arrival distribution reflects each individual's decision to arrive according to their own ability to maximise their fitness. This is a demonstration of how individual-level behaviours drive population-level behaviours.

### 2.4.3 The mate opportunity hypothesis alone is insufficient as an explanation of the evolution of protandry

The fourth result the models show is the mate opportunity hypothesis is likely to be insufficient on its own as an explanation of the evolution of protandry but the fifth result is the mate opportunity hypothesis combined with the susceptibility hypothesis may provide sufficient explanation for the evolution of protandry and protogyny.

With equal survival for both sexes the mate opportunity model shows equal mean arrival dates but female distribution is slightly wider than males, this means the first females arrive before the first males and actually indicates the evolution of protogyny. It seems unlikely on the assumptions of the mate opportunity model, with early arrival costly for females, that females should arrive before males. Perhaps if the shape of the distribution of arrival times throughout the population had been allowed to vary as opposed to being fixed at a symmetric normal distribution an alternative outcome may have occurred. If the distribution was able to evolve the female population may have adopted a positively skewed shaped distribution where the majority of the population could arrive as it does in the results here but first arriving females would not be forced by the distribution shape to arrive so extremely early and before the males. It seems likely that a skewed population distribution would have allowed the female population to achieve a higher fitness and may have shown the evolution of protandry instead of the strange mix of equal mean arrival dates for both sexes but wide female distribution. This is a limitation of the model but also an interesting result because it shows the importance of fully understanding the distribution of a population to establish the presence and degree of protandry. Evidence seems to imply migratory arrival times may follow a normal distribution but the results here suggest there could be a skew in the arrival of protandrous species (Hüppop & Hüppop, 2004). If male and female distributions of arrival times in nature were different from each other this would also complicate the model. Kokko (2006) assumed early arrival was beneficial to females due to an increased opportunity for sperm competition through EPCs. If the female function of the mate opportunity model presented here is reversed to have the model more similar to the of Kokko (2006) the model shows no difference for male or female biased survival but interestingly shows the evolution of protogyny when survival is equal between the sexes as mean female arrival is 2 days before mean male arrival (full methods and results are detailed in appendix 4). This further indicates that an evolving distribution would be interesting for future study.

The suggestion that the shape of population distributions influences protandry raises a point for the empirical measurement of protandry as it suggests the all the individuals in the population have a role to play in determining the presence and degree of protandry. Commonly protandry is measured empirically as the difference between the arrival of the first observed male and the first observed female of the population. This is inherently inaccurate however because it is sometimes difficult to tell sexes apart and assumes observed birds are from the same mate groups (Spottiswoode *et al.* 2006; Raino *et al.* 2007). The difference between arrival strategies of male and female populations may be more than the difference in days between the first arriving male and the first arriving female but it may also be more than the difference between the mean male or female arrival. Useful mathematical work for the future would be to allow the distributions of the model to evolve, this would establish how important the distributions of the population arrival times are to the evolution of protandry and would provide insight onto which population parameters are most useful to record to accurately identify and measure protandry.

### 2.4.4 The rank advantage and mate opportunity hypotheses combined may explain the evolution of protandry

The final result the models show is although rank advantage and mate opportunity are insufficient individually to explain the evolution of sex differences in arrival dates, combined together they provide a possible mechanism for the evolution of protandry. The final model, the integrated model of rank advantage and mate opportunity hypothesis, clearly shows protandry occurs under equal survival conditions; mean male arrival is 2 days before mean female arrival and male distribution is wider than females so the majority of males arrive before the majority of females (figure 2.12a). This suggests that territorial species whose males gain an advantage of early arrival through EPCs or mate multiply are likely to evolve protandry. This is supported with evidence from the pied flycatcher, where males benefit from early arrival for increased territory quality and increased opportunity for fitness gains resulting from EPCs (Canal *et al.* 2012). Similar support is demonstrated in barn swallows and eastern kingbirds (Møller, 1994; Cooper *et al.* 2011). The susceptibility hypothesis was not investigated in any of these studies, which would have provided useful data to compare the sex biased models with because the models show when survival is male biased protandry evolves and as the conditions become more biased in favour of males the degree of protandry increases.

The final result the models show is the rank advantage hypothesis, when combined with the susceptibility hypothesis, may be a stronger force on the evolution of protandry than the mate opportunity combined with the susceptibility hypothesis. Comparing the results of the rank advantage model and mate opportunity models separately, when a male bias is present the rank advantage model produces the biggest difference in mean arrival dates between the sexes and also the biggest difference in distributions; it appears that rank advantage has a stronger influencing force over the evolution of protandry when combined with the susceptibility hypothesis than the mate opportunity model. Then considering the integrated model that combines both rank advantage and mate opportunity hypotheses final distributions, particularly male arrivals, are much closer to those of the rank advantage model than the mate opportunity model. This indicates that when environmental conditions are a strong factor in driving arrival dates, early arrival to gain territory is more likely to cause protandry to evolve or increase the degree of protandry than early arrival for increased mating opportunities.

### 2.4.5 Conclusion

The models presented here explore the balance between natural and sexual selection forces with the aim of exploring potential mechanisms for the evolution of protandry in migratory avian species. The models indicate an optimum arrival date exists for both sexes and these can be conflicting. The models show that protandry in avian species may be explained by the rank advantage hypothesis combined with either the susceptibility hypothesis or the mate opportunity hypothesis. The models also show the mate opportunity hypothesis combined with the susceptibility hypothesis or all three hypotheses combined may be further explanations for the evolution of protandry. These results show territorial species that mate multiply or whose males benefit from EPCs are likely candidates for the evolution of protandry. This likelihood increases if the species also show a large degree of sexual dimorphism or some other bias that renders females more susceptible to poor conditions early in the season at a breeding ground than males. The models show that the methods for measuring protandry are important, as individual strategies are important for determining the effects on the population. They indicate that a combination of first arrival and mean or median arrival dates may be best used in combination for measuring protandry. The models also show that if a benefit to early arrival is through territory acquisition or increased mating opportunities this may be enough to advance the arrival dates of the entire population to earlier in the season even if protandry does not evolve.

Perhaps the most important result of the model is showing the very large effect environment has on the evolution of protandry. This is particularly interesting in light of climate change throughout the 20th and 21st century. Many empirical studies have shown that climate change may advance arrival dates in migratory birds but advancement in arrival dates does not always directly match advancement of climate (Knudsen *et al.* 2011). Perhaps the different responses of the sexes to similar environments could play a role in species adaptation to environmental effects such as climate change. This is what I move onto in chapter three.

## CHAPTER 3

# The effects of climate change on protandrous migratory avian species

## 3.1 Introduction

The mean temperature of the world has increased by 0.6˚C over the last century and this has been correlated with changes in behaviour throughout the animal kingdom (Root et al. 2003). Changes in the timing of significant lifetime events appear to be the most common responses of all to global warming. While some species are showing a limited ability to adapt they are likely to be left weakened and susceptible to other factors (Walthner et al. 2002; Root et al. 2003; Parmesan, 2006). It is generally agreed that global warming advances avian migratory arrival dates but very little is known about the effect global warming may have on protandry or the mechanisms behind these effects (Knudsen et al. 2011).

The main result of Chapter 2 showed that the interplay of natural and sexual selection forces is likely to make protandrous species susceptible to changes in environment. This next chapter provides the opportunity to explore how exactly protandrous avian species may react to environmental change, specifically climate change. This work is important because identifying the changes that may occur in protandrous species as they are faced with climate change will be useful in identifying the most at-risk species.

### 3.1.1 Global warming affects migratory species

Climate change affects the life-timings, including migrations, of species across the taxa (Walthner et al. 2002). The greylag goose (*Anser anser*) is a classic example of a species that has shown an advancement of its spring migration time from winter in Holland to spring in Norway since 1971 as climate has warmed (Pistorius et al. 2006). Many other species of birds including European songbirds and North American passerines have also shown an advancement of breeding and migration dates over the last century correlated with rises in global temperature (Crick et al. 1997; Ivanauskas et al. 1997; Bradley et al. 1999; Crick & Sparks 1999; Butler 2003; Hüppop & Hüppop 2004; Lehikoinen et al 2004; Marra et al. 2005; Rainio et al. 2007; Ruboilinio et al. 2007; Thorup et al. 2007). Few clear-cut patterns in the cause of advancement have been uncovered however; often the degree arrival dates have advanced by does not directly match the degree of advancing spring (Knudsen et al. 2011). For example the European pied flycatcher (*Ficedula hypoleuca*) has advanced its egg laying date to earlier in the season over the last 20 years but not at the same rate that spring arrival has advanced (Coppack & Both, 2008). Many of the examples of avian migratory adaptation to climate change appear to be driven by different mechanisms; global factors, local factors, geographic effects, resource mis-match effects and changes to migratory route as examples (Ahola et al. 2004; Knudsen et al. 2011). The large variety of mechanisms already observed in different species indicates the nature of adaptation to global warming by adjusting naturally and sexually selected traits is likely to be complex (Coppack & Both, 2008).

Some studies have demonstrated larger responses to climate change in birds that have long migratory journeys than those with shorter journeys (MacMynowski & Root, 2007). Global warming has affected seasonal food distributions and this has affected migratory dates; a study of white fronted geese (*Anser albifrons albifrons*) showed their ability to shift migration dates to follow the early arrivals of food resources related to global warming (van Wijk et al. 2012).

Some evidence suggests that birds that exhibit high levels of sexual selection may have an increased ability to adapt to climate change. One study of nine protandrous European migratory species showed a correlation between the level of sexual selection in each species and the degree to which arrival dates have advanced over the last 30 years with those showing highest levels of sexual selection advancing most (Spottiswoode et al., 2006). Another study showed barn swallow (*Hirundo rustica*) males advanced their migratory dates more than females (Møller 2004). This study also showed average tail length of male swallows, a sexually selected trait, increased simultaneously. The authors suggest arrival date advancing and tail length increasing are an example of strengthening sexual selection in the face of weakening natural selection. Of note species that show high levels of sexual dimorphism in body size and colourings generally show higher levels of protandry anyway (Rubolini et al. 2004; Raino et al. 2007; Coppack et al. 2006).

### 3.1.2 The effect of global warming on protandrous arrival is largely unknown

Protandry is theorised to be driven by a different balance of natural and sexual selection in each sex, as a result it is theorised that protandrous species could be susceptible to changes in environment such as global warming (Morbey & Ydenberg, 2001; Ahola et al. 2004; Kokko et al. 2006; Coppack et al. 2006; Raino et al. 2007; Chapter 2 of this thesis). This susceptibility to environmental change may arise from differences between sexes including body size and ability of the larger sex to tolerate poor conditions better or length of migratory journey as males often winter closer to breeding grounds than females (Rainio et al. 2007, Ketterson & Nolan, 1976; Catry et al. 2005; Komar et al. 2005).

Evidence regarding the effect of global warming on protandry is conflicting; a large study of barn swallows showed a strong association between increasing degree of protandry with climate change (Møller 2004) but a meta study of data from four other protandrous species, redstart (*Phoenicurus phoenicurus*), red backed shrike (*Lanius collurio*), blackcap (*Sylvia atricapilla*) and pied fly catcher (*Ficedula hypoleuca*), showed an advancement of arrival dates in all four that correlated with global warming but no effect on the degree of protandry (Rainio et al. 2007). Studies of protandry are further complicated by the difficulties in measuring protandry; many species are difficult to sex from observations which makes it difficult to ensure observed birds are from the same breeding population and there is also controversy over the use of mean, median or first arrival dates as the most appropriate measure. (Spottiswoode et al. 2006; Raino et al, 2007). These difficulties have already been discussed in Chapter 2. Here the degree of protandry is generally measured as the differences between male and female mean arrival dates. This is not the most accurate measure for all scenarios of population distributions however so when a scenario occurs where this is obviously inappropriate they are discussed individually.

### 3.1.3 Mathematical models of protandry and climate change

There are many empirical studies examining the effect of global warming on migration generally and there are a series of mathematical models to complement these studies, each using very different methods and considering unique factors. There are however few empirical studies of the effect of global warming on avian protandry or the effects of sex differences on response to global warming and accordingly there are no mathematical models of either.

Modelling techniques used for investigating migration arrival dates include thermodynamic models such as General Circulation Models and Global Vegetation Models (Malcolm et al. 2002). These models examine the effect of increasing levels of atmospheric $CO_2$ on migration using world climate databases and mapping actual migration routes considering the effects of real structures such as lakes and cities the birds would encounter. These models have shown global warming will be disruptive to migration and species most likely to survive are those who can adapt to speed up their migrations and shorten their journey time.

Game theory has been used to consider the effects of climate change when arrival affects territory quality (Jonzen *et al*. 2007). This is similar to the rank advantage hypothesis detailed in Chapter 2 but treats the population as homogenous rather than divided into two sexes. Jonzen *et al*. 2007 showed that if highest availability of food and optimal environmental conditions occurred on different dates when a species expected them to occur simultaneously then the optimal arrival date for that species became difficult to predict. They concluded that the optimal arrival date of the species is unlikely to advance as much as the date of the highest availability of food; perhaps indicating that other environmental factors are bigger drivers of protandry than food availability alone. A follow-up model showed that the optimal arrival date would not necessarily match the optimal environmental conditions either and that the peak of optimal environmental conditions and the peak of arrival dates may be highly variable and may actually move away from each other (Johansson & Jonzen, 2012).

Another approach to modelling migration is through the use of annual routine models. Annual routine models, also commonly used in modelling life histories, consider the behaviour and condition of the individual at stochastic time intervals throughout the season (McNamara & Houston, 2008). Some annual routine models have specifically considered how changing availability of food resources under global warming may affect optimal migration time and optimal time to moult feathers (Barta et al. 2006; Barta et al. 2007). Another annual routine model accounts for factors on individual birds such as current location, body condition, risk of predation, ability to forage, moult state and energy requirements and shows climate change will affect the number of offspring an individual has but not when it decides to moult (Hedenström et al. 2007).

Johansson et al. (2012) present a model of food resources and migratory arrival. This model does not include protandry. They use a logistic curve as an estimate of survival rate due to environmental conditions and natural selection and a reverse logistic curve for individual reproduction dependant on food availability. They assume the earlier an individual arrives the more opportunity it has to eat food and so it is likely to have a higher number of offspring and they use adaptive dynamic techniques to allow the population to evolve with the invasion of mutant forms and settle to an evolutionary stable strategy (ESS). They compare each ESS under scenarios of advanced spring versus advanced food distribution as climate change may produce. They conclude that ecological 'mismatching' of arrival and resources is a real threat to avian populations. They also conclude through the consideration of winter survival and pre-breeding season survival that the responses of a population to climate change is subject to many factors and small change in parameters can produce large changes in population dynamics. Of note although similar in logic and use of logistic curves this model is significantly different to my models detailed in Chapter 2; Johansson et al. (2012) assume a homogenous population that does not include protandry whereas my models are specifically designed to consider the effects of differential natural and sexual selection on each sex and the sex differences in arrival timings that result. Also Johansson et al. (2012) assumed a uniform distribution of arrival dates whereas my models assume a normal distribution but more importantly my model allows this distribution to evolve as individuals change their strategies for arrival.

These models detailed above are all useful and all contribute in some way to the understanding of how climate change affects migration. Some however, particularly the annual routine models, are very complicated. In their closing remarks Johansson et al. (2012) call for further realism through more use of, and testing models on, real data and using more complex parameters. They particularly want to make their logistic model closer to an annual routine model that can include interspecies competition for nesting sites, the effects of changes in the differences between arrival and breeding dates and intimate details of the migration route and conditions. I do not agree that more complex modelling is required yet, I argue the opposite because of the conflicting evidence from different species regarding hypothesis for timing in arrival; simpler modelling with few parameters is required to build models that can discern the major effects which can then be tested by empirical studies.

### 3.1.4 Aims

A degree of variation in mean annual temperature between years is to be expected however in the last hundred years the degree in variation of mean annual temperature between years and mean annual temperature have been increasing (Walthner et al. 2002; Root et al. 2003; Parmesan, 2006; Raino et al. 2007). The results of models presented in

Chapter 2 revealed that the evolution of protandry in migratory avian species is likely to be highly susceptible to changes in environmental conditions such as climate change. So the aim of this work is to investigate how changes in environment, specifically climate change, may affect the evolution of arrival dates in protandrous avian species. This is examined in two parts, first how changes in the degree of variation in annual temperatures may affect the evolution of protandry and second how an increasing mean annual temperature may affect the evolution of protandry.

## 3.2 Methods

### 3.2.1 Assumptions of climate change

The climate has been warming at an unexpectedly high rate over the last 100 years (Walthner et al. 2002; Root et al. 2003; Parmesan, 2006). The general global warming has caused extremes of weather and makes predicting weather between years and seasons increasingly uncertain particularly as the effects are not constant across areas (Giorgio & Francisco, 2000; Root et al. 2003). Evidence for this increasing variation is also seen in the increasing variation of oscillatory weather indices, such as the North Atlantic Oscillation, which are important indicators of changes in pressure differentials that drive the weather (Scaiffe et al. 2005; Osborn, 2006). How this increasing uncertainty and variation in temperature and resulting environmental conditions affects species is relatively unknown and how this variation may affect migratory birds specifically is even less understood (Stireman et al. 2005; Knudsen et al. 2011). It is the increasing between year variation in conditions and the increasing mean temperatures that are the target of investigation here.

### 3.2.2 The survival curve, $S(t)$, and midpoint, $b$.

For all models in Chapter 2 (summarised in appendix 9 for ease of reference), survival due to environmental conditions is summarised by the survival function:

$$s(t) = \frac{1}{1 + e^{-a(t-b)}}$$

(Eqn 3.1)

This function gives a sigmoidal curve which represents how probability of survival increases from 0 to 1 over the course of the season. The rate this change happens is dictated by the slope, controlled by parameter $a$, and how early or late in the season this happens, controlled by parameter $b$. The parameter $b$ is the midpoint of the $s(t)$ curve; an individual who arrives on day $t = b$ achieves a 50% probability of survival. It is this midpoint $b$ which is manipulated here to simulate climate change (figure 3.1a). If $b$ decreases this is biologically equivalent to mean temperature of the environment increasing and thus survival increasing because temperature and survival at the breeding ground are known to be positively associated (Ketterson & Nolan, 1976; Myers, 1981; Morbey & Ydenberg, 2001).

### 3.2.3 Simulating climate change by manipulating model parameter *b*

Every time a model is used it is run for 300 years, assuming one generation per year, and may have a different value of $b$. In this chapter different patterns of change of $b$ over the 300 years are used to test different elements of climate change on each of the environment, rank advantage, mate opportunity and integrated models from Chapter 2. In the first part of this study a noise generating function is used to create between year variation in values of $b$ over the 300 years of each model run. This simulates the increasingly unpredictable environment and resulting unpredictable survival rates that climate change brings (figure 3.1b). The second part of this study combines the random variation in $b$ with a generally decreasing mean value of $b$. This simulates the general warming of temperatures that climate change brings and combines this with the increasing unpredictable elements of climate change (figure 3.1c).

Mathematically, yearly values of $b$ are summarised as:

$$b_T = b_{mean} + r b_\sigma$$

(Eqn 3.2)

Where $T$ is the year number, $b_{mean}$ is the average expected value of $b$, $r$ is a random number generating function which chooses numbers randomly from a normal distribution with mean of 0 and standard deviation of 1 and $b_\sigma$ is the standard deviation in between year variation in $b$ (MathWorks, 2014).

### 3.2.4 Testing the susceptibility hypothesis on all models

The susceptibility hypothesis was investigated in Chapter 2 by testing all models with equal survival between the sexes, male biased survival and female biased survival using different shaped survival curves (figure 2.7). Testing the susceptibility hypothesis using different shaped survival curves is inappropriate here because of the use of the random number generator to select $b$ values; it would be difficult to ensure a bias was consistent across all years. Instead, the susceptibility hypothesis is included in this chapter by first testing all models assuming equal survival between the sexes where;

$$b_m = b_f$$

(Eqn 3.3)

And second by assuming there is a male survival bias such that males achieve a 50% chance of survival twenty days earlier than females every year (figure 3.1d);

$$b_m = b_f - 20$$

(Eqn 3.4)

Only a male survival bias is tested because male biased survival is thought to be more common in birds than female biased survival and also because in Chapter 2 it was never shown for a female biased survival to result in protandry (Owens & Bennet, 1995; Møller *et al.* 2004). Initially models were run with various levels of difference but for small differences, e.g. 5 days, the differences in arrival time were negligible.

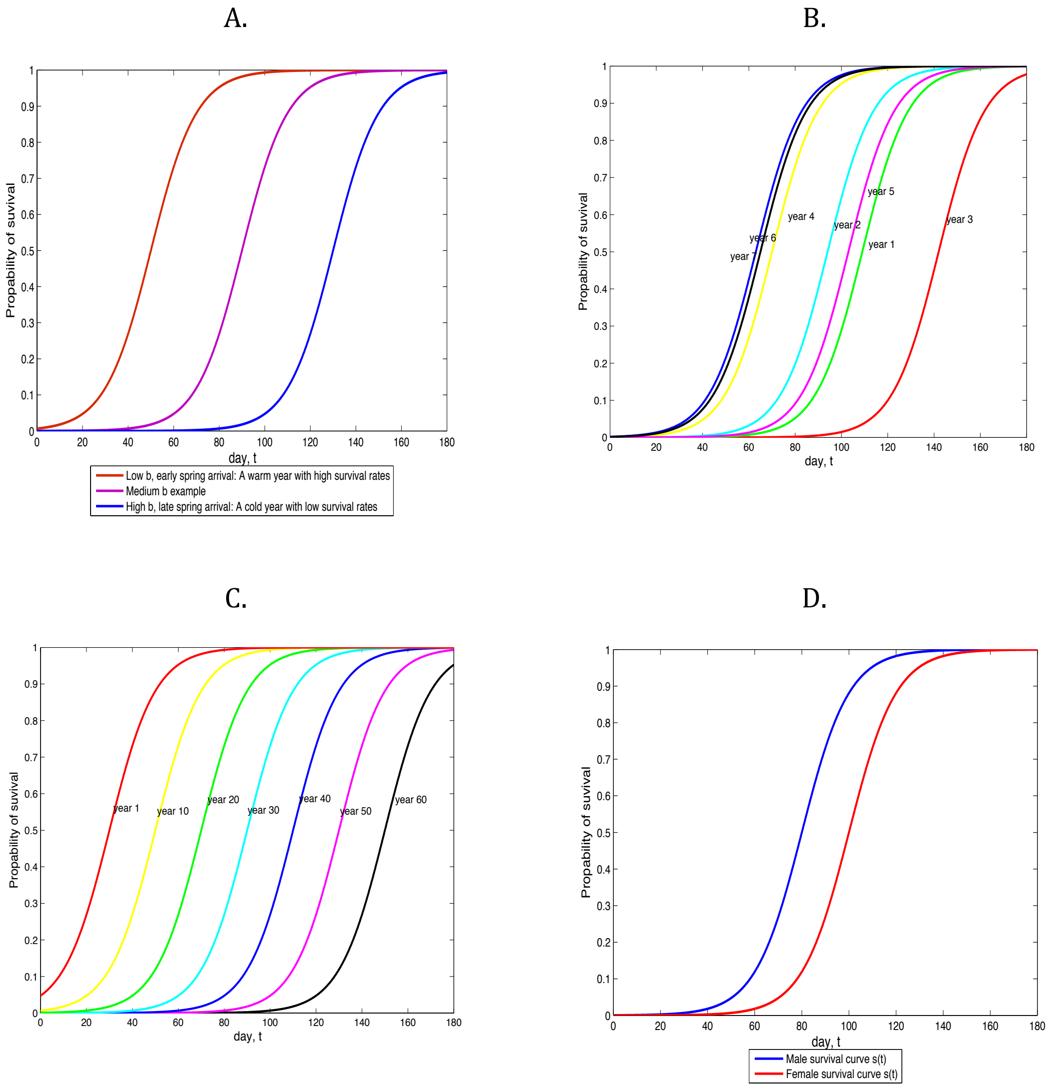

**Figure 3.1: Parameter *b* is the target of manipulation**

A. **Decreasing parameter *b* simulates a warmer environment with higher survival rates.** When $b$ is low spring arrives early in the season and on average survival rates are high. When $b$ is high winter conditions persist at the breeding ground for a long time and on average survival rates are low.
B. **Random variation produces random values of *b* each year.** Values of $b$ are randomly selected from a range of normally distributed arrival dates each year. The size of the range of possible $b$ values can be manipulated. Note this example is exaggerated for illustrative purposes.
C. **Increasing mean annual temperature is simulated with a linearly decreasing *b*.** To simulate a warming climate, the mean value of $b$ decreases each year. Note this example is exaggerated for illustrative purposes.
D. **The effect of the male survival bias.** Males always achieve a fifty per cent chance of survival 20 days earlier than females. Note these survival curves are different from the functions used to illustrate male biased survival in chapter 2 because they have $a_m = a_f = 0.1$.

### 3.2.5 Statistical analysis of simulations

A single simulation for any model was run for 300 generations, which was long enough for both populations to evolve to stable equilibria. For each model, under every scenario and control, simulations were repeated thirty times and the final male and female mean arrival dates and standard deviations, $\mu_m$, $\sigma_m$, $\mu_f$ or $\sigma_f$, of each population were recorded.

The results of each set of simulations within each scenario of climate change was analysed for significant deviation from its respective control using a 2 sample t-test. The null hypothesis stated that mean of the scenario simulations was equal to the expected value the control presented and the alternative hypothesis was that they were not equal. Results were further tested using a 2 sample t-test to compare the difference between male and female mean arrival date within each scenario. This ensured no incidences of evolving protandry were missed because evolved male or female arrival was not significantly different from its control.

Simulations were created using random variations in climate and the effect of the randomness is part of the focus of this study, as such care was taken to ensure each single simulation result was inspected for outliers as these outliers may be lost in comparing differences between the means of groups but may provide noteworthy reflections on the effect of random values of $b$. The results that follow are one set of results for demonstration. A sensitivity analysis revealed similar results for a wide range of values locally around the parameters used in this set and so this set of results may be considered representative of the model's behaviour.

## 3.3 Part one: The effect of random between year variation in $b$

### 3.3.1 Random between year variation in $b$ reflects an unpredictable environment

In part one of this chapter it is assumed there is between year variation in $b$ but the mean value of $b$ over all 300 years is fixed. This simulates the unpredictable environment caused by climate change. For comparison, every model is run under control A; a fixed value of $b$ that does not vary between years. All models are then tested under scenarios 1a and 1b which test the effect of a degree of between year variation in $b$ at a low level and a high level of variation. The second scenario tests the effect of increasing the degree of variation from low to high over the 300 years of the simulation on each model. Examples of the values $b$ may take for each of these scenarios is illustrated in figure 3.2. Models are tested first assuming equal survival between the sexes and then with male biased survival.

#### *Control A: No between year variation in b.*

The value of $b$ is the same every year (figure 3.2a).

The male value of $b$ is set to a medium value;

$$b_m = 90$$

(Eqn 3.5)

Recall for every control and scenario of every model $b_f$ was tested first assuming equal survival between the sexes, $b_f = b_m$, and second assuming male biased survival, $b_f = b_m + 20$.

#### *Scenario 1a & b: Some between year variation in b.*

Scenarios 1a and 1b test the models when a degree of variation is present in yearly values of $b$. The mean value of $b$ is 90 over the 300 years but each year the value of $b$ may be higher or lower than this, moving the survival curve later or earlier in the season.

The male value of $b$ is calculated with;

$$b_m = 90 + r b_\sigma$$

(Eqn 3.6)

Where $r$ generates random numbers each year from a normal distribution with mean zero and standard deviation of one. The parameter $b_\sigma$ is a measure of the possible range of values parameter $b_m$ may deviate around day 90. Scenario 1a tests the models with a low degree of between year variation where $b_\sigma = 5$ and scenario 1b tests the models with a high degree of between year variation where $b_\sigma = 10$ (figure 3.2b).

### *Scenario 2: Increasing between year variation in b.*

Scenario 2 tests the models when the degree of variation in yearly values of $b$ increases from low to high however the mean value of $b$ still remains at 90 over the 300 years.

The male value of $b$ is calculated with;

$$b_m = 90 + r \frac{T}{300} b_{\sigma\_max}$$

(Eqn 3.7)

Parameter $T$ is the year or generation number, $b_{\sigma\_max}$ is the maximum range of values parameter $b_m$ may deviate around. Scenario 2 is tested when $b_{\sigma\_max} = 10$ (figure 3.2c).

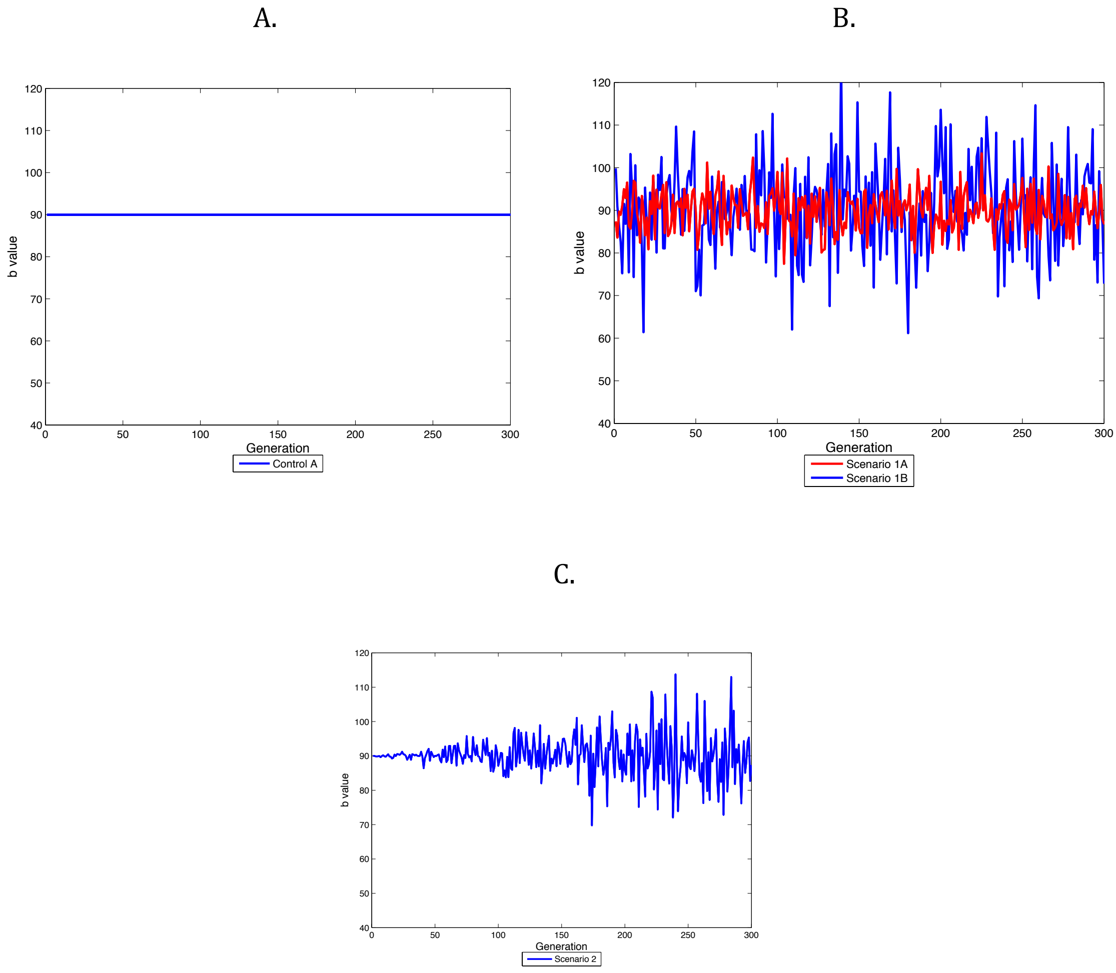

**Figure 3.2: Scenarios of between year variation in *b* value in part 1**

- **A.** **Yearly *b* values used in control A**. Mean value of *b* is 90 over the duration of each simulation and there no between year variation in *b* occurs.
- **B.** **Example pattern of yearly *b* values a simulation may create under scenarios 1a and 1b.** Mean value of *b* is 90 over the duration of each simulation but between year variation in *b* is present at a low degree (scenario 1a) and a high degree (scenario 1b).
- **C.** **Example pattern of yearly *b* values a simulation may create under scenario 2.** Mean value of *b* is 90 over the duration of each simulation but between year variation in *b* occurs. Degree of variation in *b* ranges from low in year 1 to high in year 300.

### 3.3.2 Results of part one

#### *Equal survival*

Control A

When survival is equal the environment, rank advantage and mate opportunity models show males and females having equal mean arrival dates. The environment and rank advantage models show the males and females having equal width population distributions. The mate opportunity model shows the females arriving with a wider distribution than males. The integrated model shows males arriving 2 days before females and with a wider distribution (table 3.1). This follows results from Chapter 2.

Scenario 1a

Neither the environment nor rank advantage model show any significant deviation from control A in scenario 1a. They show no evolution of protandry in any individual simulation either. The mate opportunity model shows no significant deviation of any parameter from control A however mean male arrival is significantly earlier than mean female arrival ($t_{58} = 4.099$; $p < 0.001$) and in some individual simulations mean male arrival is up to 2 days before females. The integrated model shows the male and female mean arrivals to be significantly earlier than control A and significantly different from each other ($t_{58} = 3.770$; $p < 0.001$), in some individual simulations however the difference between mean arrivals is decreased to zero (table 3.1).

Scenario 1b

Neither the environment nor rank advantage model show any significant deviation from control A in scenario 1b nor do they show evolution of protandry in any individual simulation either. The mate opportunity model shows no significant deviation of any parameter from control A however mean male arrival is significantly earlier than mean female arrival ($t_{58} = 3.917$; $p < 0.001$) and in some individual simulations mean male arrival is up to 2 days before females. The integrated model shows the male and female mean arrivals to be significantly earlier than control A and significantly different from each other ($t_{58} = 2.107;\ p = 0.039$). The integrated model also shows female distribution to be wider than control A. In some individual simulations the difference between mean arrivals is decreased from two to zero and the mean difference between male and female arrivals is decreased from scenario 1a (table 3.1).

### Scenario 2

Neither the environment nor rank advantage model show any significant deviation from control A in scenario 1b nor do they show evolution of protandry in any individual simulation either. The mate opportunity model shows no significant deviation of any parameter from control A however mean male arrival is significantly earlier than mean female arrival ($t_{58} = 3.202;\ p = 0.002$) and in some individual simulations mean male arrival is up to 2 days before females. The integrated model shows the male and female mean arrivals to be significantly earlier than control A and mean arrival is different from each other but this is not quite significant ($t_{58} = 1.750;\ p = 0.085$). The integrated model also shows female distribution to be wider than control A. In some individual simulations the difference between mean arrivals is decreased from two to zero and the mean difference between male and female arrivals is decreased from scenario 1a and 1b (table 3.1).

**Table 3.1 Average final population distributions of control A and scenarios 1a, 1b and 2 with equal survival between the sexes**

Average final values of each simulation set for each scenario are provided, those that are significantly different from control A are highlighted red. Difference between the mean values of male and female arrival dates and range of differences that occurred throughout the individual simulations are also included, where mean difference in male and female arrival is significantly different in the scenario from the control it is highlighted in red.

|  | Mean simulation values | Control A | Scenario 1a | Scenario 1b | Scenario 2 |
|---|---|---|---|---|---|
| Environ-ment model | $\mu_m$ | 109 | 108.20 | 108.67 | 108.47 |
|  | $\sigma_m$ | 26.2 | 26.13 | 26.03 | 26.14 |
|  | $\mu_f$ | 109 | 108.20 | 108.67 | 108.47 |
|  | $\sigma_f$ | 26.2 | 26.13 | 26.03 | 26.14 |
|  | Mean $\mu_f - \mu_m$ | 0 | 0 | 0 | 0 |
|  | Range of $\mu_f - \mu_m$ | - | 0 | 0 | 0 |
| Rank advantage model | $\mu_m$ | 87 | 86.93 | 87.40 | 86.27 |
|  | $\sigma_m$ | 17.2 | 17.15 | 17.24 | 17.24 |
|  | $\mu_f$ | 87 | 86.93 | 87.40 | 86.27 |
|  | $\sigma_f$ | 17.2 | 17.15 | 17.24 | 17.24 |
|  | Mean $\mu_f - \mu_m$ | 0 | 0 | 0 | 0 |
|  | Range of $\mu_f - \mu_m$ | - | 0 | 0 | 0 |
| Mate opportunity model | $\mu_m$ | 109 | 107.73 | 108.00 | 107.07 |
|  | $\sigma_m$ | 19.4 | 19.37 | 19.33 | 19.41 |
|  | $\mu_f$ | 109 | 109.33 | 109.93 | 108.80 |
|  | $\sigma_f$ | 20.8 | 20.79 | 20.77 | 20.81 |
|  | Mean $\mu_f - \mu_m$ | 0 | 1.6 | 1.933 | 1.733 |
|  | Range of $\mu_f - \mu_m$ | - | 0→2 | 0→2 | 0→2 |
| Integrated model | $\mu_m$ | 81 | 73.2 | 69.27 | 70.00 |
|  | $\sigma_m$ | 13.6 | 13.61 | 13.63 | 13.65 |
|  | $\mu_f$ | 83 | 74.27 | 70.20 | 70.87 |
|  | $\sigma_f$ | 8.8 | 8.90 | 9.06 | 9.06 |
|  | Mean $\mu_f - \mu_m$ | 2 | 1.066 | 0.933* | 0.8667** |
|  | Range of $\mu_f - \mu_m$ | - | 0→2 | 0→2 | 0→2 |

*Difference from control A is not quite significant at the 95% confidence level, p-value = 0.082

** Difference from control A is not quite significant at the 95% confidence level, p-value = 0.064

## *Male biased survival*

### Control A

When survival is male biased the environment, rank advantage and mate opportunity models all show mean male arrival date to be earlier than mean female arrival date by 16, 18 and 18 days respectively. Distribution width is widest for males in the environment model and widest for females in the mate opportunity model however there are no extreme differences and there are no complications of overlapping populations. The integrated model shows mean male and female arrival dates to be equal but shows male distribution to be much wider than females (table 3.2).

### Scenario 1a

The environment model showed a significant increase in difference between mean arrival dates in scenario 1a against control A. The rank advantage model showed no significant deviation from control A in scenario 1a. Both environment and rank advantage models show some individual scenarios to increase the difference between mean arrivals by 2 days. The mate opportunity model shows mean arrival of both sexes to be significantly later than control A, males by 9.47 days and females by 8.8 days. The mate opportunity model also shows male and female distributions to be significantly narrower than control A but not by a large degree ($\sigma_m$ decreases from 22.6 to 21.76, and $\sigma_f$ decreases from 23.2 to 22.03). The integrated model shows no significant difference in any final value from control A, however mean male and female arrival do decrease slightly and male arrival is now significantly earlier than female arrival ($t_{58} = 4.059$; $p < 0.001$). Individual simulations in the integrated model show difference in mean arrival varying between 0 and 2 days (table 3.2).

### Scenario 1b

The environment model shows no significant difference in any final value from control A in scenario 1b but some individual scenarios show an increase in mean difference between male and female arrivals of up to 2 days. The rank advantage model shows no significant difference in mean arrivals but does show female distribution to be significantly wider than control A, although this difference is small ($\sigma_f$ increases from 17.0 to 17.21). Some individual scenarios of the rank advantage model show an increase in mean difference between male and female arrivals of up to 2 days. The mate opportunity model shows mean arrival of both sexes to be significantly later than control A, males by 8.4 days and females by 8 days. The mate opportunity model also shows male and female distributions to be significantly narrower than control A but by an even smaller degree than in scenario 1a ($\sigma_m$ decreases from 22.6 to 21.84 and $\sigma_f$ decreases from 23.2 to 22.15). Some individual scenarios of the mate opportunity model under scenario 1b show the difference between mean arrivals to decrease from 18 to 16 days. The integrated model shows no significant difference in any final value from control A however mean male and female arrival do increase slightly and male arrival is now significantly earlier than female arrival ($t_{58} = 2.089$; $p < 0.001$). Individual simulations in the integrated model show difference in mean arrival varying between 0 and 2 days (table 3.2).

### Scenario 2

The environment model shows no significant difference in any final value from control A in scenario 2 but some individual scenarios show an increase in mean difference between male and female arrivals of up to 2 days. The rank advantage model shows no significant difference in mean arrivals but does show female distribution to be significantly wider than control A, although this difference is small ($\sigma_f$ increases from 17.0 to 17.81). Some individual scenarios of the rank advantage model show an increase in mean difference between male and female arrivals of up to 2 days. The mate opportunity model shows mean arrival of both sexes to be significantly later than control A, males by 8.47 days and females by 7.93 days. The mate opportunity model also shows male and female distributions to be significantly narrower than control A but not by an even smaller degree than in scenario 1a ($\sigma_m$ decreases from 22.6 to 21.83 and $\sigma_f$ decreases from 23.2 to 22.07). Some individual scenarios of the mate opportunity model under scenario 2 show the difference between mean arrivals to decrease from 18 to 16 days. The integrated model shows no significant difference in any final value from control A however mean male and female arrival do increase slightly and male arrival is now significantly earlier than female arrival ($t_{58} = 2.671$; $p < 0.001$). Individual simulations in the integrated model show difference in mean arrival varying between 0 and 4 days (table 3.2).

**Table 3.2 Average final population distributions of control A and scenarios 1a, 1b and 2 with male biased survival.**

Average final values of each simulation set for each scenario are provided, those that are significantly different from control A are highlighted red. Difference between the mean values of male and female arrival dates and range of differences that occurred throughout the individual simulations are also included, where mean difference in male and female arrival is significantly different in the scenario from the control it is highlighted in red.

| | Mean simulation values | Control A | Scenario 1a | Scenario 1b | Scenario 2 |
|---|---|---|---|---|---|
| Environment model with male biased survival | $\mu_m$ | 109 | 107.33 | 109.20 | 108.33 |
| | $\sigma_m$ | 26.2 | 26.23 | 25.90 | 26.15 |
| | $\mu_f$ | 125 | 124.60 | 126.00 | 125.20 |
| | $\sigma_f$ | 22.4 | 22.51 | 22.27 | 22.45 |
| | Mean $\mu_f - \mu_m$ | 16 | 17.267 | 16.8 | 16.867 |
| | Range of $\mu_f - \mu_m$ | - | 16→18 | 16→18 | 16→18 |
| Rank advantage model with male biased survival | $\mu_m$ | 87 | 87.40 | 87.07 | 87.27 |
| | $\sigma_m$ | 17.2 | 17.17 | 17.25 | 17.25 |
| | $\mu_f$ | 105 | 106.07 | 106.13 | 105.80 |
| | $\sigma_f$ | 17 | 17.12 | 17.21 | 17.18 |
| | Mean $\mu_f - \mu_m$ | 18 | 18.667 | 19.0667* | 18.533 |
| | Range of $\mu_f - \mu_m$ | - | 18→20 | 18→20 | 18→20 |
| Mate opportunity model with male biased survival | $\mu_m$ | 83 | 92.47 | 91.40 | 91.47 |
| | $\sigma_m$ | 22.6 | 21.76 | 21.84 | 21.83 |
| | $\mu_f$ | 101 | 109.80 | 109.00 | 108.93 |
| | $\sigma_f$ | 23.2 | 22.03 | 22.15 | 22.07 |
| | Mean $\mu_f - \mu_m$ | 18 | 17.33 | 17.6 | 17.467 |
| | Range of $\mu_f - \mu_m$ | - | 16→18 | 16→18 | 16→18 |
| Integrated model with male biased survival | $\mu_m$ | 83 | 81.20 | 82.07 | 80.93 |
| | $\sigma_m$ | 13.8 | 13.83 | 13.90 | 13.90 |
| | $\mu_f$ | 83 | 82.93 | 83.73 | 82.93 |
| | $\sigma_f$ | 9.6 | 9.47 | 9.54 | 9.52 |
| | Mean $\mu_f - \mu_m$ | 0 | 1.733 | 1.667 | 2 |
| | Range of $\mu_f - \mu_m$ | - | 0→2 | 0→2 | 0→4 |

* Difference from control A is not quite significant at the 95% confidence level, p-value = 0.082

## 3.4 Part Two: The effect of decreasing mean value of *b*

### 3.4.1 Decreasing mean value of *b* reflects a warming environment

In part two it is assumed there is between year variation in $b$ but also the mean value of $b$ over all 300 years is decreasing. This simulates the unpredictable environment climate change causes and simulates the general warming of global temperatures. Every model is first run under control B; a decreasing value of $b$ that does not vary between years. All models are then run under scenarios 3a and 3b which test the effect of a degree of between year variation in $b$, at a low level and a high level of variation, on top of assuming the mean value of $b$ is decreasing over the course of the simulation. The fourth scenario tests the effect of increasing the degree of variation from low to high as the value of $b$ is decreasing through each simulation. Examples of the values $b$ may take for each of these scenarios is illustrated in figure 3.3. Models are tested first assuming equal survival between the sexes and then with male biased survival.

#### *Control B: No between year variation in b but decreasing mean value of b.*

The value of $b$ is the decreasing slightly every year (figure 3.3a).

The male value of $b$ each year is;

$$b_m = 90 - \frac{T}{15}$$

(Eqn 3.8)

When survival is equal between the sexes the mean values of $b_m$ and $b_f$ is day 90. When survival is male biased $b_m$ starts at 90 and $b_f$ starts at 110, because $b_f = b_m + 20$, this decreases to day 70 and 90 respectively by the end of the simulation.

#### *Scenario 3a & 3b: Some between year variation in b and decreasing mean value of b.*

Scenarios 3a and 3b test the models when a degree of variation is present in yearly values of $b$ and mean value of $b$ is decreasing through the simulation. The mean value of $b_m$ starts at 90 but decreases to 70 in the 300th year but the actual value of $b_m$ each year may be higher or lower than this moving the survival curve earlier or later in the season depending on random variations.

The male value of $b$ is calculated with;

$$b_m = 90 - \frac{T}{15} + r b_\sigma$$

(Eqn 3.9)

Scenario 3a tests the models with a low degree of between year variation where $b_\sigma = 5$ and scenario 3b tests the models with a high degree of between year variation where $b_\sigma = 10$ (figure 3.3b).

### *Scenario 4: Increasing between year variation in b and decreasing mean value of b.*

Scenario 4 tests the models when the degree of variation in yearly values of $b$ increases from low to high and the mean value of $b$ decreases from 90 to 70 over the 300 years of each simulation.

The male value of $b$ each year is;

$$b_m = 90 - \frac{T}{15} + r \frac{T}{300} b_{\sigma\_max}$$

(Eqn 3.10)

Scenario 2 is tested when $b_{\sigma\_max} = 10$ (figure 3.3c).

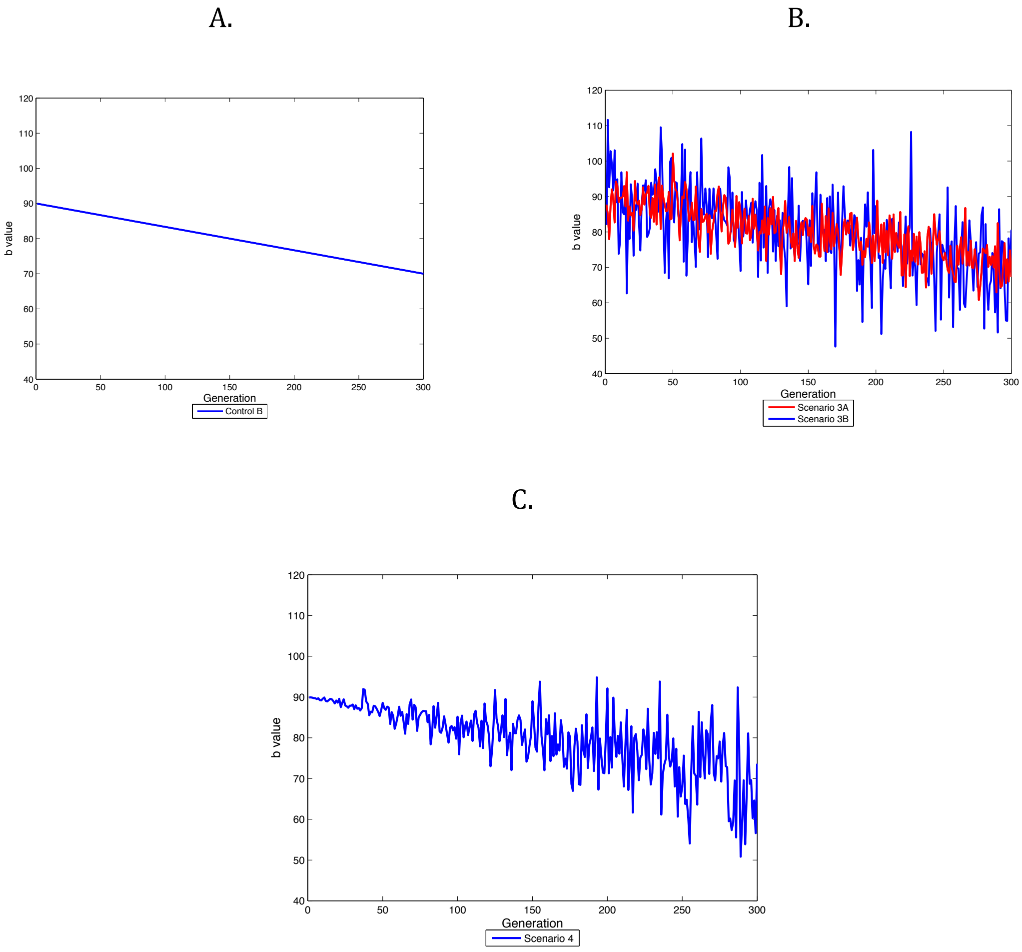

**Figure 3.3: Scenarios of between year variation and decreasing mean value of *b* in part 2**

- **A. Yearly *b* values used in control B**. Mean value of $b_m$ decreases from 90 to 70 over the duration of each simulation. There is no random between year variation in $b$.
- **B. Example pattern of yearly *b* values a simulation may create under scenarios 3a and 3b.** Mean value of $b_m$ decreases from 90 to 70 over the duration of each simulation and between year variation in $b$ is present at a low degree (scenario 3a) and a high degree (scenario 3b).
- **C. Example pattern of yearly *b* values a simulation may create under scenario 4.** Mean value of $b_m$ decreases from 90 to 70 over the duration of each simulation and between year variation in $b$ increases each years. Degree of variation in $b$ ranges from low in year 1 to high in year 300.

### 3.4.2 Results of part 2: The effects of a warming climate advancing the survival curve

#### *Equal survival*

##### Control B

When survival is equal the environment, rank advantage, mate opportunity and integrated models show males and females having equal mean arrival dates. The environment and rank advantage models show the males and females having equal width population distributions. The mate opportunity model shows the females arriving with a wider distribution than males.

The integrated model shows males and females to have equal mean arrival dates but males arriving with a much wider distribution than females (table 3.3). This contrasts with the results of chapter 2 where males arrived 2 days earlier than females as well as having a wider distribution than them when survival was equal under the integrated model (figure 2.12a). Notably if the model is modified such that $b$ does not decrease to as low a value (for example using $b_m = 110 - \frac{T}{15}$ instead) then male arrival follows the pattern of that in chapter 2 where males arrive earlier than females and with a wider distribution. This effect is likely caused because as $b$ becomes sufficiently low the conditions are such that early arrival is equally favourable for both sexes; the benefits of early arrival to the females outweigh the costs at low values of $b$ in the integrated model. This argument is strengthened because of the difference in mean arrival date of males and females seen under scenarios 3a, 3b and 4 for the integrated model; these scenarios still show protandry because the average value of $b$ is not as low as in control B due to the effect of noise.

##### Scenario 3a

The environment model shows no significant difference in mean arrival dates but shows male and female distributions to be significantly narrower than control B although this difference is small (both $\sigma_m$ and $\sigma_f$ decrease from 30.2 to 29.9). The environment model shows no difference in mean arrival in any individual simulation. The rank advantage model shows no significant difference in any parameter between scenario 3a and control B, no individual scenario shows any difference in mean arrival dates. The mate opportunity model shows no significant deviation from control B for any final value but male mean arrival is slightly earlier and female mean arrivals is slightly later than control B and mean male arrival has become significantly earlier than female arrival ($t_{58} = 4.269$; $p < 0.001$). The integrated model shows the male and female mean arrivals to be significantly earlier than control A, males by 5.4 days and females by 4.1 days; male arrival is also now significantly earlier than female arrival ($t_{58} = 3.211$; $p < 0.001$). Male arrival distribution is significantly narrower in scenario 3a than in control B ($\sigma_m$ decreases from 13.6 to 13.4) but this difference is small. In some individual simulations of the integrated model the difference between mean arrivals varies between 0 and 2 days (table 3.3).

### Scenario 3b

The environment model shows no significant difference in mean arrival dates but shows male and female distributions to be significantly narrower than control B although this difference is small (both $\sigma_m$ and $\sigma_f$ decrease from 30.2 to 29.51). The environment model shows no difference in mean arrival in any individual simulation. The rank advantage model shows no significant difference in any parameter between scenario 3b and control B, no individual scenario shows any difference in mean arrival dates. The mate opportunity model shows no significant deviation from control B for any final value but male and female mean arrivals are slightly later than control B and mean male arrival has become significantly later than female arrival ($t_{58} = 3.560$; $p < 0.001$). Mean difference between male and female arrival can vary by up to 2 days in the mate opportunity model. The integrated model shows the male and female mean arrivals to be significantly earlier than control B, males by 10.13 days and females by 8.93 days. Male arrival is now significantly earlier than female arrival ($t_{58} = 2.681$; $p < 0.001$). In some individual simulations of the integrated model the difference between mean arrivals varies between 0 and 2 days (table 3.3).

### Scenario 4

The environment model shows no significant difference in mean arrival dates but shows male and female distributions to be significantly narrower than control B although this difference is small ($\sigma_m$ decreases from 30.2 to 29.61 and $\sigma_f$ decreases from 30.2 to 29.561). The environment model shows no difference in mean arrival in any individual simulation. The rank advantage model shows no significant difference in any parameter between scenario 4 and control B, no individual scenario shows any difference in mean arrival dates either. The mate opportunity model shows no significant deviation from control B for any final value but male and female mean arrivals are slightly later than control B and mean male arrival has become significantly later than female arrival ($t_{58} = 3.444$; $p = 0.001$). Mean difference between male and female arrival is always 2 days under the mate opportunity model. The integrated model shows the male and female mean arrivals to be significantly earlier than control A, males by 9.27 days and females by 8.13 days. Male arrival is now significantly earlier than female arrival ($t_{58} = 2.257$; $p = 0.028$). In some individual simulations of the integrated model the difference between mean arrivals varies between 0 and 2 days (table 3.3).

**Table 3.3 Average final population distributions of control B and scenarios 3a, 3b and 4 with equal survival between the sexes.**

Average final values of each simulation set for each scenario are provided, those that are significantly different from control B are highlighted red. Difference between the mean values of male and female arrival dates and range of differences that occurred throughout the individual simulations are also included, where mean difference in male and female arrival is significantly different in the scenario from the control it is highlighted in red.

| | Mean simulation values | Control B | Scenario 3a | Scenario 3b | Scenario 4 |
|---|---|---|---|---|---|
| Environment model | $\mu_m$ | 91 | 91.00 | 91.60 | 91.20 |
| | $\sigma_m$ | 30.2 | 29.90 | 29.51 | 29.61 |
| | $\mu_f$ | 91 | 91.00 | 91.60 | 91.20 |
| | $\sigma_f$ | 30.2 | 29.90 | 29.51 | 29.61 |
| | Mean $\mu_f - \mu_m$ | 0 | 0 | 0 | 0 |
| | Range of $\mu_f - \mu_m$ | - | 0 | 0 | 0 |
| Rank advantage model | $\mu_m$ | 67 | 68.27 | 68.53 | 68.53 |
| | $\sigma_m$ | 17.2 | 17.16 | 17.25 | 17.26 |
| | $\mu_f$ | 67 | 68.27 | 68.53 | 68.53 |
| | $\sigma_f$ | 17.2 | 17.16 | 17.25 | 17.26 |
| | Mean $\mu_f - \mu_m$ | 0 | 0 | 0 | 0 |
| | Range of $\mu_f - \mu_m$ | - | 0 | 0 | 0 |
| Mate opportunity model | $\mu_m$ | 91 | 90.40 | 90.47 | 91.67 |
| | $\sigma_m$ | 21 | 21.01 | 20.98 | 20.91 |
| | $\mu_f$ | 91 | 91.87 | 92.40 | 93.67 |
| | $\sigma_f$ | 24.8 | 24.78 | 24.59 | 24.49 |
| | Mean $\mu_f - \mu_m$ | 0 | 1.4 | 1.93 | 2 |
| | Range of $\mu_f - \mu_m$ | - | 0→2 | 0→2 | 2 |
| Integrated model | $\mu_m$ | 63 | 57.60 | 52.87 | 53.73 |
| | $\sigma_m$ | 13.6 | 13.48 | 13.55 | 13.56 |
| | $\mu_f$ | 63 | 58.60 | 54.07 | 54.87 |
| | $\sigma_f$ | 8.8 | 8.79 | 8.92 | 8.91 |
| | Mean $\mu_f - \mu_m$ | 0 | 1 | 1.2 | 1.133 |
| | Range of $\mu_f - \mu_m$ | - | 0→2 | 0→2 | 0→2 |

### *Male biased survival*

#### Control B

When survival is equal the environment, rank advantage, mate opportunity and integrated models show mean male arrival date to be earlier than mean female arrival by 18, 20 and 16 days respectively. In the environment model male distribution is widest, in the rank advantage model male and female distributions are equal and in the mate opportunity model female arrival distribution is slightly wider than males. The integrated model under control B shows equal mean male and female arrival dates but male distribution is much wider than females (table 3.4). Similar to when survival was equal for control B this is likely to be because sustained low values of $b$ create favourable conditions for both species to arrive early. If $b$ does not decrease so sharply or so far throughout the season then protandry remains under control B with a male sex bias in the integrated model.

#### Scenario 3a

The environment model shows no significant difference in mean arrival dates but shows male and female distributions to be significantly narrower than control B although this difference is small ($\sigma_m$ decreases from 30.2 to 29.87 and $\sigma_f$ decreases from 26.2 to 25.91). The environment model shows some simulations vary in difference between male and female days from 16 to 18 days, a slight decrease. The rank advantage model shows no significant difference in any parameter between scenario 3a and control B but individual scenarios may show a difference in male and female mean arrival dates that varies between 18 to 20 days. The mate opportunity model shows females to arrive 5 days later in scenario 3a than control B and males to arrive with a significantly narrower distribution ($\sigma_m$ decreases from 22.2 to 21.76). The integrated model shows no significant difference in male and female mean arrival dates from control B but male arrival is slightly earlier and female arrival is slightly later and this is enough to make the difference between the sexes significant in the simulations ($t_{58} = 3.538$; $p < 0.001$). Individual simulations can show variation in difference from mean arrival between 0 and 4 days (table 3.4). The integrated model also shows male distribution to be slightly wider in scenario 3a than control B ($\sigma_m$ decreases from 13.6 to 13.73).

### Scenario 3b

The environment model shows no significant difference in mean arrival dates but shows male population distribution to be significantly narrower than control B although this difference is small ($\sigma_m$ decreases from 30.2 to 29.63). The environment model shows some simulations vary in difference between male and female days from 16 to 18 days. The rank advantage model shows no significant difference in any parameter between scenario 3b and control B but individual scenarios may show a difference in male and female mean arrival dates that varies between 18 to 20 days. The mate opportunity model shows mean arrival of both sexes to be significantly later than control B, the males by 2.93 days and the females by 4.53 days. Both sexes arrive with a significantly narrower distribution than control B ($\sigma_m$ decreases from 22.2 to 21.87 and $\sigma_f$ decreases from 22.4 to 22.35). Individual simulations of the mate opportunity model under scenario 3b may show a difference in male and female mean arrival dates that varies between 16 to 18 days. The integrated model shows no significant difference in male and female mean arrival dates from control B but mean arrival of both sexes from the simulations is slightly later than control B and the difference between the two mean arrival dates is significant ($t_{58} = 3.286$; $p = 0.002$) Individual simulations can show variation in difference from mean arrival between 2 and 6 days (table 3.4). The integrated model also shows male distribution to be slightly wider in scenario 3b than control B ($\sigma_m$ increases from 13.6 to 13.81).

### Scenario 4

The environment model shows no significant difference in mean arrival dates but shows male and female distributions to be significantly narrower than control B although this difference is small ($\sigma_m$ decreases from 30.2 to 29.5 and $\sigma_f$ decreases from 26.2 to 25.71).

The environment model shows some simulations vary in difference between male and female days from 16 to 18 days. The rank advantage model shows no significant difference between mean arrival dates in scenario 4 and control B but male distribution is significantly wider ($\sigma_m$ increases from 17.2 to 18.02). Individual scenarios may show a difference in male and female mean arrival dates that varies between 18 to 20 days in the rank advantage model. The mate opportunity model shows female arrival to be 4.47 days later than in control B but there are no other significant difference for the other parameters. Individual scenarios may show a difference in male and female mean arrival dates that varies between 16 to 18 days in the mate opportunity model under scenario 4. The integrated model under scenario 4 shows female distribution to be significantly later by 12.47 days than control B; female arrival is now significantly later than male arrival ($t_{58} = 6.871$; $p < 0.001$). Individual simulations show the difference between mean arrival dates to vary between 4 and 12 days (Table 3.4). The integrated model also shows male and female arrival distributions to be significantly wider than control B ($\sigma_m$ increases from 13.6 to 14.65 and $\sigma_f$ increases from 9.4 to 10.73).

**Table 3.4 Average final population distributions of control B and scenarios 3a, 3b and 4 with male biased survival.**
Average final values of each simulation set for each scenario are provided, those that are significantly different from control B are highlighted red. Difference between the mean values of male and female arrival dates and range of differences that occurred throughout the individual simulations are also included, where mean difference in male and female arrival is significantly different in the scenario from the control it is highlighted in red.

| | Mean simulation values | Control B | Scenario 3a | Scenario 3b | Scenario 4 |
|---|---|---|---|---|---|
| Environment model with male biased survival | $\mu_m$ | 91 | 91.07 | 90.27 | 92.60 |
| | $\sigma_m$ | 30.2 | 29.87 | 29.63 | 29.50 |
| | $\mu_f$ | 109 | 108.60 | 107.87 | 109.67 |
| | $\sigma_f$ | 26.2 | 25.91 | 25.96 | 25.71 |
| | Mean $\mu_f - \mu_m$ | 18 | 17.533 | 17.6 | 17 |
| | Range of $\mu_f - \mu_m$ | - | 16→18 | 16→18 | 16→18 |
| Rank advantage model with male biased survival | $\mu_m$ | 67 | 68.73 | 68.67 | 69.40 |
| | $\sigma_m$ | 17.2 | 17.17 | 17.28 | 18.02 |
| | $\mu_f$ | 87 | 88.13 | 87.60 | 88.60 |
| | $\sigma_f$ | 17.2 | 17.15 | 17.27 | 17.99 |
| | Mean $\mu_f - \mu_m$ | 20 | 19.4 | 18.933* | 19.2 |
| | Range of $\mu_f - \mu_m$ | - | 18→20 | 18→20 | 18→20 |
| Mate opportunity model with male biased survival | $\mu_m$ | 89 | 92.47 | 91.93 | 92.00 |
| | $\sigma_m$ | 22.2 | 21.76 | 21.87 | 21.83 |
| | $\mu_f$ | 105 | 110.00 | 109.53 | 109.47 |
| | $\sigma_f$ | 22.4 | 22.05 | 22.35 | 22.10 |
| | Mean $\mu_f - \mu_m$ | 16 | 17.533 | 17.6 | 17.4667 |
| | Range of $\mu_f - \mu_m$ | - | 16→18 | 16→18 | 16→18 |
| Integrated model with male biased survival | $\mu_m$ | 63 | 62.67 | 63.40 | 66.80 |
| | $\sigma_m$ | 13.6 | 13.73 | 13.81 | 14.65 |
| | $\mu_f$ | 63 | 64.60 | 65.67 | 75.47 |
| | $\sigma_f$ | 9.4 | 9.40 | 9.51 | 10.73 |
| | Mean $\mu_f - \mu_m$ | 0 | 1.933 | 2.267 | 8.667 |
| | Range of $\mu_f - \mu_m$ | - | 0→4 | 2→6 | 4→12 |

* Difference from control B is not quite significant at the 95% confidence level, p-value = 0.082

## 3.5 A summary of all results

### 3.5.1 The controls

Control A changed no aspect of environment; it produced the same patterns of arrival as seen in Chapter 2. Control B, where yearly value of *b* decreased slightly every year to simulate warming temperature, showed all final arrival dates for all models to be significantly earlier than in control A, except for the mate opportunity model with male biased survival. In summary advancing *b* advances arrival dates of both sexes.

### 3.5.2 The environment model

The environment model with male biased survival showed males to arrive 16 days before females in control A and 18 days in control B. The environment model under scenarios 3a and 4 caused male and female arrival distributions to be narrower than control B with both equal survival and male biased survival. Scenario 3b caused both to be narrower when survival was equal but only male arrival to be significantly narrower when survival was male biased (Tables 3.3 and 3.4).

In summary, adding only variation in *b* had no effect on the environment model. Decreasing the mean value of *b* caused populations to arrive early in the season. Combining variation in *b* with a decreasing mean value of *b* caused populations to arrive early and with a significantly wider distribution. Decreasing the mean value of *b* over the year appears to have a larger effect on arrival distributions than increasing the degree of variation in values of *b* between years.

### 3.5.3 The rank advantage model

The rank advantage model with male biased survival showed males to arrive 18 days before females in control A and 20 days before females in control B. With male biased survival, scenarios 1b and 2 showed female arrival distribution to widen (Table 3.2). When survival was male biased only scenario 4 showed any significant difference from control B; male and female populations arrived with a wider distribution (Table 3.4). There were no notable outliers for any of the simulations of the rank advantage model, however all scenarios showed up to 2 days variation in individual simulations in the number of days males arrived before females when survival was male biased.

In summary the rank advantage model is fairly resistant to changes in yearly values of *b*. The climate scenarios cause very little effect on the rank advantage model.

### 3.5.4 The mate opportunity model

In both control A and B with equal survival females arrived with a wider distribution than males but equal mean arrival dates. The mate opportunity with male biased survival showed males to arrive 18 days before females in control A and 26 days before females in control B. The mate opportunity model with male biased survival showed significant effect for all scenarios; all scenarios caused mean female arrival date to be later than the control predicted and scenarios 1a, 1b, 2 and 3b caused male mean arrival date to be later than the control predicted. For all scenarios with male biased survival there was between 0 and 2 days difference between male and female mean arrival dates predicted by the control and actual difference of each simulation (Tables 3.2 and 3.4). When survival is male biased and the value of *b* gradually decreases through the year, as in control B and scenarios 3a, 3b and 3c, the mean arrival of both sexes is generally later in the season than is predicted if *b* is constant, as in control A and scenarios 1a, 1b and 2.

In summary, when survival is equal between the sexes the mate opportunity model is fairly resistant to climate scenarios, however in some individual simulations a slight difference in mean male and female arrival dates did occur demonstrating an underlying potential for the evolution of protandry given the right conditions but the probability of this occurring is small. The climate scenarios cause general arrival dates of both sexes to advance under the mate opportunity model. The mate opportunity model with male biased survival is susceptible to variation in between year values of *b* but maybe less susceptible to decreasing mean values of *b*. Decreasing the value of *b* appears to have less of an impact on arrival distributions than increasing the degree of variation in values of *b* between years.

### 3.5.5 The integrated model

The integrated model with equal survival showed significant advancement of mean arrival dates for both sexes for all climate scenarios compared to the dates the controls predicted. With equal survival control A predicts protandry for the integrated model. Control B still predicts protandry but to a lesser degree; male and female arrival dates are equal but male distribution is still much wider than female distribution (Table 3.3). Under all scenarios with equal survival protandry is predicted. When survival is male biased, scenarios 1a, 1b and shows no significant effect on either arrival dates or distribution but within individual simulations the difference in mean arrival date may vary between 0 and 4 days (Table 3.2). When survival is male biased, scenarios 3a, 3b and 4 show significant widening of the male arrival distribution. Scenario 4 also shows female to arrive significantly later and with a wider distribution. The male biased models show a larger degree in variation of difference between male and female arrival dates within individual simulations; for example scenario 4 shows difference may vary from 4 to 12 days in some simulations (Table 3.4).

In summary the integrated model with equal survival appears more generally susceptible to climate change scenarios than the integrated model with male biased survival but the effects of climate change scenarios appear to be bigger when survival is male biased. The climate scenarios cause general arrival dates of both sexes to advance. The integrated model shows the potential for large effects of climate change on the evolution of protandry.

## 3.6 Discussion

Models of environment, rank advantage, mate opportunity and integrated hypotheses were tested for the effects of climate change in two parts; the first part tested the effect of between year variation in $b$ and the second part combined yearly variation with a decreasing mean value of $b$. This was done to simulate global warming and uncertainty in yearly temperatures climate change may bring. Although there is evidence many avian species can adjust migration dates in line with climate change, the mechanisms of how this happens is however not well understood (Knudsen et al. 2011). The work presented here appears to be the first use of modelling to consider the effect of climate change on protandry in avian migration.

### 3.7.1 Climate change advances general arrival dates

The first obvious result this chapter shows is that a generally warming environment, simulated with a decreasing $b$, generally advances the arrival of migratory species under the environment, rank advantage, mate opportunity and interated models with equal survival. This is also true of the environment, rank advantage and integrated models with a male survival bias. Evidence for the advancement of arrival dates due to climate change is seen widely across species of migratory birds, protandrous or otherwise, across the globe so while this is not a novel result it is a good start(Crick et al. 1997; Ivanauskas et al. 1997; Bradley et al. 1999; Crick & Sparks 1999; Butler 2003; Hüppop & Hüppop 2004; Lehikoinen et al 2004; Marra et al. 2005; Rainio et al. 2007; Ruboilinio et al. 2007; Thorup et al. 2007, as detailed in section 3.1.1). Møller et al. (2010) hypothesise that birds benefit from early arrival in the face of climate change because it allows them a longer breeding season and associated increase of offspring production and survival this brings. Although this may be a contributing factor the rest of the results here suggest advancement of arrival is more complicated than this.

### 3.7.2 Climate change has a stronger effect when survival is male biased

The models illustrate that climate change has a more significant effect on protandry and general arrival times when a survival bias occurs because a larger number of significant differences occur for all scenarios when survival is male biased. Chapter 2 showed that protandry would evolve when the rank advantage or mate opportunity hypotheses were combined with the susceptibility hypothesis. This is maintained in Chapter 3 but the rank advantage hypothesis combined with the susceptibility hypothesis is much less affected by changes in climate than the mate opportunity hypothesis combined with the susceptibility hypothesis. A study of nine protandrous species showed that how far they advanced their migratory arrival dates in response to climate change was positively associated with the degree of sexual selection in each species (Spottiswoode et al., 2006). If degree of sexual selection provides any indicator of degree of the effect of the susceptibility hypothesis it seems logical that species where the susceptibility hypothesis contributes to the explanation for the evolution of protandry should be more affected by climate change than those that don't and this is what the models confirm.

### 3.7.3 The rank advantage hypothesis is resistive to climate change

The rank advantage hypothesis appears fairly resistant to changing environment either as a stand-alone hypothesis of protandry or combined with the susceptibility hypothesis. Chapter 2 showed protandry will evolve if the rank advantage hypothesis is combined with the susceptibility as male biased survival. The results here in Chapter 3 indicate that the susceptibility hypothesis is still the main driver of protandry in territorial species and climate change has very little effect. When survival is equal a generally warming temperature shows species under the rank advantage hypothesis arriving generally earlier but does not cause protandry to evolve. When survival is male biased protandry evolves under the rank advantage hypothesis but no significant difference in degree of protandry occurs unless high level of variation in climate has been sustained for a long time (as in scenario 1b and 3b; tables 3.2 and 3.4). When a general warming of climate is included the model with equal survival shows a much larger advancement of female arrival dates than the male biased model. This is reflective of the diminished survival females achieve on the same day in the male biased model.

The rank advantage combined with the susceptibility hypothesis however remains a potential explanation for the evolution of protandry and in the face of a generally warming climate the expected degree of protandry increases by two days.

### 3.7.4 Climate change may cause protandry to evolve under the mate opportunity hypothesis

Chapter 2 shows the mate opportunity hypothesis alone does not lead to the evolution of protandry; it shows mean arrival to be equal but first arriving individuals to be female. This was concluded to illustrate a potential limit of the model, which was the inability of the shape of the population distribution to evolve. The results here in Chapter 3 however show whenever environment is disturbed by any of the scenarios of change in *b* the male arrival evolves to be significantly earlier than female arrival.

Protandry in the pied flycatcher (*Ficedula hypoleuca*) appears to be driven by the mate opportunity hypothesis although they are also a territorial species (Canal *et al.* 2012). Arrival dates in this species are known to be associated with temperatures but as a long distant migrant they cover many areas which are differently affected by climate change and this is expected to make them particularly susceptible to the variation in environment climate change brings (Hüppop & Winkel, 2006). All the models here for the mate opportunity suggest that environmental variation will increase the degree of protandry, regardless of any survival bias but this is for a maximum of two days and depends on the random variation in climate.

An unexpected result of the model is that while both controls and all scenarios demonstrate protandry in the mate opportunity model when the mate opportunity model is combined with the susceptibility hypothesis as male biased survival, arrival is later in control B for both sexes than control A. Adding between year variation in all scenarios shows male and female arrival to be later in the season. This could show the males matching female arrival; females choose to arrive much later because they achieve good survival later so males do not need to arrive as early as they otherwise would have. This is an example of the interaction between natural and sexual selection forces; natural selection drives female arrival and sexual selection drives male arrival in response to female arrival.

### 3.7.5 Climate change has the largest effect when rank advantage, mate opportunity hypotheses and susceptibility hypotheses are combined

Chapter 2 shows that the mate opportunity and rank advantage hypotheses combined may provide an explanation for the evolution of protandry. The results here in Chapter 3 show the integrated model with equal survival evolves protandry but only to a small degree and only when variation in climate reaches a high level. The results here also show that the integrated model with a male survival bias, rank advantage, mate opportunity and susceptibility hypotheses combined, is affected by variations in climate more than any other model and this is likely to cause protandry to evolve. The largest degree of protandry is caused when the integrated hypothesis is male biased, climate is warming and between year uncertainty is increasing. In this scenario male arrival may evolve to be between 4 and 12 days earlier than females, this is highly significant (scenario 4; table 3.4).

The Møller (2004) study of barn swallows, whose protandry appears to be explained by both the rank advantage and mate opportunity hypotheses, showed males responded more to climate change than females. This is reflected in the outcome of the integrated model; but only when a male survival bias is present. The integrated model under scenarios of climate change shows protandry to evolve because mean male arrival is earlier than mean female arrival but also because male population distribution is wider than female population distribution. This highlights the role the shape of the population distribution may play in species adaptation and further highlights the importance of collecting data on the whole population distribution in studies of protandry not just date of mean arrival or first arrival.

### 3.7.6 Future work

Further work for the future could be to examine the effects of climate change in the geographic range of protandrous migratory avian species, for example to consider potential changes to migratory routes or stopover sites of migratory avian species. Some studies exist considering the effect of climate change on the geographic distribution of insect species who show protandry in date of adult emergence from pupae and have shown that climate change, particularly through creation of extreme climactic values can limit this range (Lynch et al. 2014). Other studies of climate change on non-protandrous migratory avian species have explored possible effects climate change may have due to changes in food distribution of $CO_2$ levels (Malcolm et al. 2002; Hedenström et al. 2007; Jonzen et al. 2007; McNamara & Housten, 2008; Johansson & Jonzem, 2012; Jonzen et al. 2012). It would be interesting to investigate whether the sexual selection hypotheses presented here, the rank advantage, mate opportunity and susceptibility hypotheses, create an opportunity for protandrous avian species to show an increased ability to evolve in response to climate change over non-protandrous migratory avian species. It would also be interesting to compare this with other species that show protandry in other life timing events such as insect emergence date (Lynch et al. 2014). A further consideration may be to combine models presented here with some assumptions of searching models of asynchronously timed species such as removing assumptions that all females will mate (Fagan et al. 2010).

### 3.7.7 Conclusion

In conclusion changes in migration of protandrous avian species should be expected as climate change continues. The models show that warming temperatures should advance arrival dates generally in protandrous migratory avian species. A high-risk group of avian species are those that show differential survival between males and females at different times at the breeding ground. Those avian species are likely to show the large changes in response to climate change. Avian species who benefit from early arrival due to territorial advantages are least likely to respond to climate change. The models predict there is a possibility that territorial avian species that do not show protandry may evolve it in the future as an adaptation to climate change. The models also predict that avian species who would benefit from early arrival due to increased mating opportunities may evolve protandry in response to climate change.

Climate change may cause an effect on the degree of protandry under each hypothesis but this effect may be small, in some cases only between 1 and 2 days difference in mean arrivals. These small changes could be easily missed unless observations are very accurate. One study has considered the effect of climate change on protandry in migratory avian species and although showed that arrival dates are generally advanced they showed no effect on degree of avian protandry (Rainio et al. 2007). There are very few studies of the effect of climate change on protandry for comparison and the results of the work here indicate that not only may the changes be small and so easily missed but the effects of climate change should be expected to be variable depending on the nature of the advantage a bird receives from early arrival. For future work it would be useful to return to classic examples of protandrous avian migration such as the barn swallows and re-examine the data or further observations of the populations ensuring recording of the arrival of the entire population. If differences were found that had previously been missed this would be interesting and if still no differences were found this would be useful feedback to refine the accuracy of the parameters of the model.

The highest risk group of migratory avian species are those that are affected by all three hypotheses; rank advantage, mate opportunity and susceptibility. This indicates species such as American redstarts, Easter kingbirds and potentially the pied flycatcher, may be particularly susceptible to changes in climate. Some simulations of the integrated model under scenario 4 showed protandry to evolve with males being up to 12 days earlier than females. In an empirically study such a finding would be massively significant and this suggests that further studies into the effects the susceptibility hypothesis and the effects of environmental change on these birds is warranted.

# Part 2

# The evolution of convenience polyandry

CHAPTER 4

# The role of female costs in the evolution of convenience polyandry

## 4.1 Introduction

This chapter presents the first model of convenience polyandry. The model is designed to explore how the forces of natural and sexual selection act along with trade-offs in female costs and benefits that cause female strategy in premating struggles to evolve. This work is important because it provides further understanding of a phenomenon that is widespread throughout the animal kingdom. Understanding convenience polyandry will help further understand the balance of natural and sexual selection in evolution.

### 4.1.1 Sexual conflict occurs over mating rate

Reproduction is never free and the costs are rarely divided equally between the sexes. Sexual conflict occurs as a subset phenomenon of sexual selection. Originally defined by Parker in 1972, sexual conflict arises when there is ‘a conflict between the evolutionary interests of individuals of the two sexes.’ Commonly sexual conflict occurs over mating rate. In 1948 Bateman theorised that male fitness may increase with the number of matings they achieve, in contrast to females whose reproductive fitness is likely limited by the production of larger, more costly gametes and so maximise fitness at a much lower mating rate than males. In this case males aim to mate at a relatively high rate and females aim to mate at a relatively low rate.

Many species show conflict over optimal mating rate and in some the divergence of male and female interests over mating rate has become so pronounced that males have evolved behaviours and morphological traits to coerce females into mating at a cost to her fitness. Extreme examples of the cost to females include sheep, frogs, solitary bees, solitary wasps and elephant seals where males are recorded to accidently kill females in their mating attempts (Geist 1971; Le Boeuf & Messnick 1990; Hiruki *et al.* 1993; Stone 1995;

Bergsten *et al.* 2001). Less extreme examples of the costs of multiple mating include *Drosophila melanogaster* and *Caenorhabditis elegans.* Multiple mating in both species is the strategy males adopt to maximise their fitness however this reduces female longevity the more matings she receives; in *D. melanogaster* this is due to the caustic seminal fluid she receives from every mating (Chapman et al., 1995; Gems & Riddle, 1996).

There are many reasons a female may suffer costs from mating conflict particularly if she has a finite amount of energy resources and must trade-off survival with reproduction. These reasons may include wasted time for the female which could otherwise be spent foraging, increased risk of predation, increased risk of disease and receipt of sex peptides that can result in reduced longevity of the female (Arnqvist 1989; Fowler & Partridge 1989; Rice 1996; Fedorka & Mousseau, 2002; Jacob & Boivin 2004; Chapman *et al.* 2005).

### 4.1.2 Sexually antagonistic coevolution of male harassment and female resistance may have lead to the evolution of convenience polyandry

In some species where sexual conflict over mating rate occurs to the point males have evolved to harass females into increasing their mating rate, females can coevolve resistance mechanisms and behaviours against the males to antagonistically decrease their mating rate (Thornhill & Alcock 1983). Examples of such pre-mating struggles where males harass resistive females for mating are particularly common in the insects (Parker, 1972; Alcock 1977; Thornhill & Alcock 1983; Otronen, 1990; Blackenhorn *et al.* 2000; Weall & Gilburn 2000; Eberhard, 2001; Cordero Rivera & Andres 2002; Perry *et al.* 2009). A classic example of the sexually antagonistic coevolution of male harassment and female resistance is in water striders (Heteroptera; Gerridae). Some species of water strider show males have evolved clasping mechanisms to grab the female and the females have evolved traits such as spines on their back or changed their body shape to avoid being grabbed (Arnqvist & Nillsson 1995; Arnqvist & Rowe, 2002).

For a resistance behaviour to be advantageous to a female it must not increase her costs in other means so they are greater than the benefits of reduced mating rate (Thornhill &

Alcock, 1989). For example if a female resists a harassive male the benefit of avoiding loss of time and energy used mating with him should not be outweighed by the costs she incurred through injury whilst resisting him. If males in a species are highly variable in 'cost to defeat' females may adopt multiple response strategies to deal with him and minimise her costs. If a male is particularly large and the female will incur high costs from resisting him and has a low probability of successfully resisting him anyway perhaps she is better to use a low cost response against the males mating attempt so she may incur the costs of copulation but lower the costs of resistance. This is *convenience polyandry*, so named because the female strategy is to accept extra matings, be polyandrous, at her convenience to minimise her costs (Thornhill & Alcock, 1983).

The first example of convenience polyandry was identified in 1977 when Alcock *et al.* demonstrated the female megachild bee (*Anthidium maculosum*) would accept matings from many males, but not all, to avoid loss of foraging time. Since this seminal study numerous examples of convenience polyandry have been reported in insects (Rowe 1991; Crean *et al.* 1999; Cordero-Rivera & Andres 2002; Blyth & Gilburn, 2006; Trontii *et al.* 2006), crustaceans (Thiel & Correa 2004; Johnson & Brockman 2010), amphibians (Sztatecsny *et al.* 2006), elasmobrachii (DiBattista *et al.* 2008; Portroy *et al.* 2008; Griffiths *et al.* 2011), reptiles (Lee & Hays 2004) and birds (Adler, 2009). The "acceptance" behaviour may be to give in completely to a male or to adopt a different low cost strategy than the usual, high cost, active resistance strategy.

### 4.1.3 The Coelopids exhibit convenience polyandry

Females of a species of European seaweed fly, *Coelopa frigida,* demonstrate convenience polyandry. Seaweed flies are found on the shoreline in wrack beds, lumps of seaweed washed up from the sea floor (Edward & Gilburn, 2007). They mate at very high frequencies in the wild and males are harassive females and a pre-mating struggle usually precedes mating (Crean et al. 1999; Blyth & Gilburn, 2006). Females have a high cost, high success response and a low cost, low success response to male harassment they appear to use depending on the male's size; they use kicking and shaking of their body to deter the male as a high cost, high success resistance response or abdomen curling as an low cost, low success response. Abdomen curling is theorised to be a much less costly behaviour than shaking or kicking but also is less successful at preventing the male from mating with her; it is a strategy reserved for particularly large males she is unlikely to dislodge with kicking and shaking (Crean & Gilburn, 1998; Crean et al. 1999; Dunn et al. 2005; Meader & Gilburn, 2008, Blyth & Gilburn, 2011).

The model here is designed with the coelopids in mind and most parameters and assumptions are drawn from studies of coelopids. However no studies exist that successfully quantifies either the cost of copulation in coelopids or the difference of costs between each resistance strategy. To draw inferences on these costs a study of the metabolic costs of mating in a species of water strider (*Aquarius remigis)* is considered. Males of *A. remigis* harass females until he can climb onto her back to mate with her, females will try to struggle and try to throw him off (Tonsi Eldakar et al. 2009). The primary cost of mating and resisting for the females is hypothesised to be the metabolic costs of the pre-mating struggle (Watson et al. 1998). In their 1998 study, Watson et al. measured the changes in $CO_2$ use of pairs of mating water striders during each mating behaviours and showed that metabolic costs increased linearly as duration of mating increased. The water strider experiment is useful because it provides initial assumptions on what shape the relationship between female response and costs could be.

### 4.1.4 The aims

Models of male harassment and female resistance exist already, exploring the sexually antagonism between the sexes that is hypothesised to result from these scenarios. Here the aim is to build on three influential models of sexually antagonistic coevolution and extend them to create the first model of convenience polyandry (Gavrilets *et al.* 2001; Rowe *et al.* 2005; Hoyle & Gilburn, 2010). Each of these original models assume female resistance is a continuous variable related to male harassment but they each only allow for a single female response strategy; active resistance. These three models assume that female fitness is driven solely by mating rate and ignore female costs. The model here builds on these important models to develop the first model of convenience polyandry; it uses the definition of resistance as a continuous variable but extends this to consider a second response strategy which is to use a high cost, high success response strategy, or a low cost, low success response strategy to a male's mating attempt. The work here adapts the original models to include female costs as a factor in determining fitness and evolution of female response. This work specifically models the seaweed fly *Coelopa frigida* however the results may be applicable to any species with pre-mating struggles where females aim to minimise cost but maximise fecundity.

## 4.2 Methods

### 4.2.1 Overview of the system

This work models the assumption of the mating system of a promiscuous system based on the coelopids. Males harass females into mating; a female may respond to a male's harassment by either using a high cost, high success response strategy or using a low cost, low success response strategy against him. The fee the female incurs from using a high cost response strategy against a male is due to her wasted energy and time and increased risk of injury. In *C. frigida*, the female high cost, high success response consists of kicking and shaking her body (Dunn et al. 1999). If a female chooses this response to a male she reduces her probability of being coerced into mating however as male size increases her chances of successfully resisting his coercion decrease. If a female uses a high cost response successfully she does not mate with the male and incurs no further costs, if a female uses a high cost response unsuccessfully she must mate with the male and incurs a further cost of copulation. In *C. frigida*, the female low cost, low success response consists of allowing the male onto her back but curling her abdomen away from him. This is a much less energetically demanding response (Dunn et al. 1999). In some species the cost of this response may be zero, in others it may be non-zero but small. Uniquely, the model here allows for testing of the cost of this response over a range of values. If a female chooses to use this low cost response against a male she incurs a small cost of the behaviour because there still may be some small amount of pre-mating engagement that uses time she could otherwise spend foraging. Choosing to use a low cost response against a male does not guarantee a female will have to mate but makes mating much more likely than had the female chosen to use a high cost response. Whichever strategy a female chooses the cost of copulation is equal. The female population may influence its fitness by the decision of which strategy is used against harassive males; high cost, high success or low cost, low success. Males experience a number of trade-offs as to optimum body size; small males attempt to mate at a higher rate but receive a high cost response from females more often and large males are more likely to overcome a female response but there is a trade-off between increasing male size and decreasing mating rate (Crean et al. 1999; Dunn et al. 1999). Male body size and female strategy choice antagonistically co-evolve as each tries to maximise their own fitness.

### 4.2.2 Female response strategy

Convenience polyandry theorises that a female chooses her response to a male harassment based on her evaluation of the cost and benefit trade-off of each response. In this model the female makes her strategy choice based on the male's size. The probability a female will choose a strategy where she uses a low cost, low success response against the male is determined by the function $\beta(x,T)$, the probability a female will choose a high costs, high success strategy against the male is given by $1-\beta(x,T)$.

$$\beta(x,T) = \frac{1}{1+e^{-s(x-T)}}$$

(Eqn 4.1)

The parameter $s$ gives the gradient and $T$ the midpoint of the function (figure 4.1a). The gradient determines the sensitivity of the female to changes in male size; a steep slope equates to high female sensitivity. The midpoint of the function determines the female threshold where a male has equal probability of receiving a high cost or a low cost strategy from the female in response to his mating harassment; a male with body size $x > T$ will be more likely to receive a low cost strategy, whereas a male with body size $x < T$ will be more likely to receive a high cost strategy (figure 4.2). Females evolve their response strategy, $\beta(x,T)$, through the evolution of their threshold, $T$, as male size, $x$, evolves to maximise their fitness.

The threshold, $T$, can range between [-∞, ∞]. If $T \rightarrow -\infty$, the females adopt a 'low cost, low success' strategy against all males as the threshold, or range of convenience polyandry, drops below actual male size. If $T \rightarrow \infty$, the females adopt a 'high cost, high success' strategy against all males.

### 4.2.3 Male mating rate

Males attempt to mate multiply but this is limited by their body size, $x$, because in the coelopids large males are less willing to mate than small males (Crean et al. 1999; Dunn et al. 1999). Of note the values of male body size, $x$, used here are measures of forelimb length which is a good indicator of male size in coelopids (Bltyh & Gilburn, 2011).

In the model here, mating rate, $\alpha(x)$, is a function of male size;

$$\alpha(x) = 1 - \frac{1}{1 + e^{-a(x-b)}}$$

(Eqn 4.2)

Similar to equation 4.1 this function is sigmoidal; $a$ determines the gradient of the slope of the curve at the midpoint and $b$ determines the midpoint of the function (figure 4.1b). The midpoint of the function is where a male of size $x$ will mate at a rate of 0.5 matings per unit time.

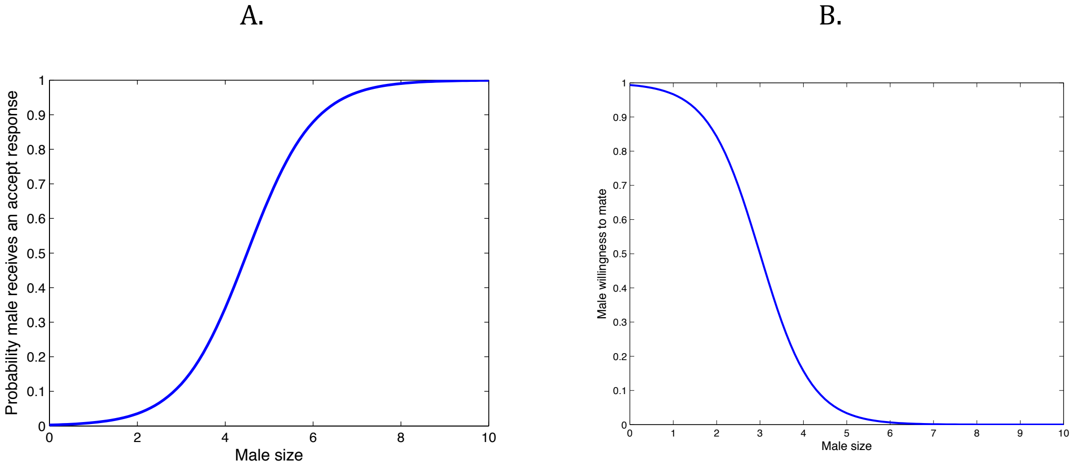

**Figure 4.1: Male mating rate and female response strategy**

A. **Female response strategy, $\boldsymbol{\beta(x,T)}$, reflects the probability a male of size $\boldsymbol{x}$ has of receiving a low cost response from a female he harasses.** The larger a male is the more likely a female is to choose to greet his harassment of her with a low cost response; the theory of convenience polyandry dictates this is to allow her to minimise her total costs of interacting with him. Here, example parameters are $s = 1.32$ and $T = 4.5$ to reflect empirical results (Blyth & Gilburn, 2011).

B. **Male mating rate, $\boldsymbol{\alpha(x)}$, decreases as his size increase.** Male mating rate is determined by a male's willingness to mate which decreases as his size increases (Dunn et al. 1999). Here, example parameters are $a = 1.68$ and $b = 3$ to reflect empirical results (Dunn et al. 1999).

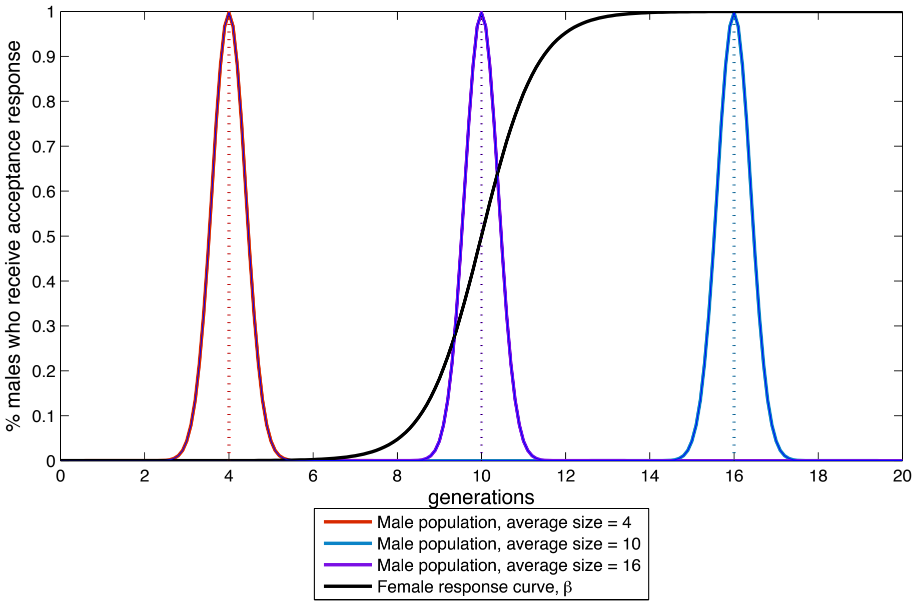

**Figure 4.2. An overlap in female response curve, $\beta(x)$, and male size distribution indicates convenience polyandry.**

An example female response curve where $s = 1.5$ and $T = 10$ is shown with 3 example male population distributions. If the male population's size distributions overlap the mixed strategy area of the female response curve convenience polyandry occurs because female response changes as male size changes. If the male population's size distributions lie below the female response curve all males receive a high cost response regardless of their size. If the male population's size distributions lie above the female response curve all males receive a low cost response regardless of size.

### 4.2.3 Female costs

Females potentially receive costly fees from three sources; males she chooses to use a high cost response against, males she chooses to use a low cost response against and copulations she is coerced to endure.

#### *Female high cost, high success response strategy fee*

Data on female costs of high cost behaviours of the coelopids is not known so here a study in water striders is used as grounds to make the relationship between male size and fee of a female high cost response linear (Watson et al. 1998). This model assumes if a female chooses to use a high cost response against a male the costs she incurs is proportionate to his body size. The fee a female pays of a high cost response depends on the male's size and is given by the linear function $\theta_F$ (figure 4.3a).

$$\theta_F = jx + k$$

(Eqn 4.3)

#### *Female low cost, low success response strategy fee*

If a female chooses to use a low cost, low success strategy against a male she incurs a small, flat rate cost; this is determined by $\theta_A$ (figure 4.3b).

#### *Female copulation fee*

Neither strategy guarantees a female protection from mating however; if the female's resistance response is unsuccessful in deterring the male she must copulate with him and incurs a cost of copulation, $\mu$. The theory of convenience polyandry assumes that this copulation fee is high and that a combination of resistance strategies are used to avoid copulation and reduce overall costs associated with mating (Thornhill & Alcock, 1983). Here $\mu$ is set at 20 units as the copulation cost for any female with any male; this should be considered a high value of $\mu$ because it is higher than the anticipated costs of reacting to most males with either a 'low cost, low success' strategy or a 'high cost, high success' strategy. To date, there exists no empirical estimate of the cost of copulation separate from costs of pre-mating struggles in coelopids.

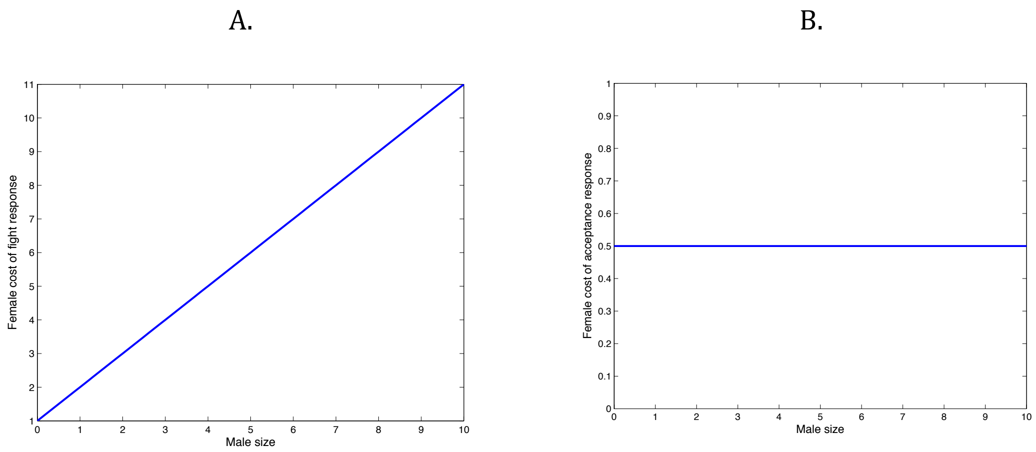

**Figure 4.3: The functions of female costs**

A. **High cost, high success strategy fee depends on male size.** Females pay a high fee of using a high cost, high success strategy against harassive male proportionate to the male's body size (Watson et al. 1998). Here, example parameters are $j = 1.25$ and $k = 1$ to reflect empirical results (Watson et al. 1998).

B. **Low cost, low success strategy incurs a flat-rate fee.** This parameter is theorised such that a low cost response behaviour, for example abdomen curling in the coelopids, is a low cost behaviour and the cost is not related to male size. The example illustrates $\theta_A = 0.5$; no empirical data exists for this parameter so examples are estimates.

### 4.2.4 The effect of male size

Males must trade-off mating rate, survival, and success over female high cost response to evolve their body size, $x$, against evolving female response strategy, $\beta(x,T)$, to maximise their fitness.

#### *Male coercion against a female high cost, high success response strategy*

Although large male size is costly in terms of mating rate in provides a benefit in reacting with resistive females because large males are better at overcoming a high cost, high success response from a female and coercing her to mate (Dunn et al. 1999; Grieve & Gilburn, unpublished data, 2011). Here, the function of male success over female high cost response is assumed to be linear. To create upper and lower limits of 1 and 0 the sigmoidal function was used to represent this but with restrictions on parameters such that the part of the curve that fell over the biologically realistic parameter space is a linear approximation (figure 4.4a). The male success over female high cost response is approximated by $\gamma_F$ where parameters $c$ and $f$ determine the slope and midpoint of this curve.

$$\gamma_F(x) = \frac{1}{1 + e^{-c(x-f)}}$$

(Eqn 4.4)

#### *Male coercion against a female low cost, low success response strategy*

Male success over securing a mating after the female has chosen to use a low cost response against him is not affected by size (Blyth & Gilburn, unpublished data, 2011); in the model this is $\gamma_A$ (figure 4.4b).

#### *Male survival*

Here, large size is also assumed to be advantageous to males because it confers an increased expected survival time. The shape of the relationship between male size and survival, driven by natural selection, is unknown in coelopids so for now is assumed to be linear. Male survival in the model is $a_1 + a_2 x$ (figure 4.4c). On the surface this may appear to produce infinitely large males that live for an infinite amount of time but generally parameters are restricted for male size between approximately 0 and 10 because it is appreciated that out with this range model male size becomes biologically irrelevant. This could be improved by using a saturation function but for mathematical simplicity a linear function with restricted parameters was chosen.

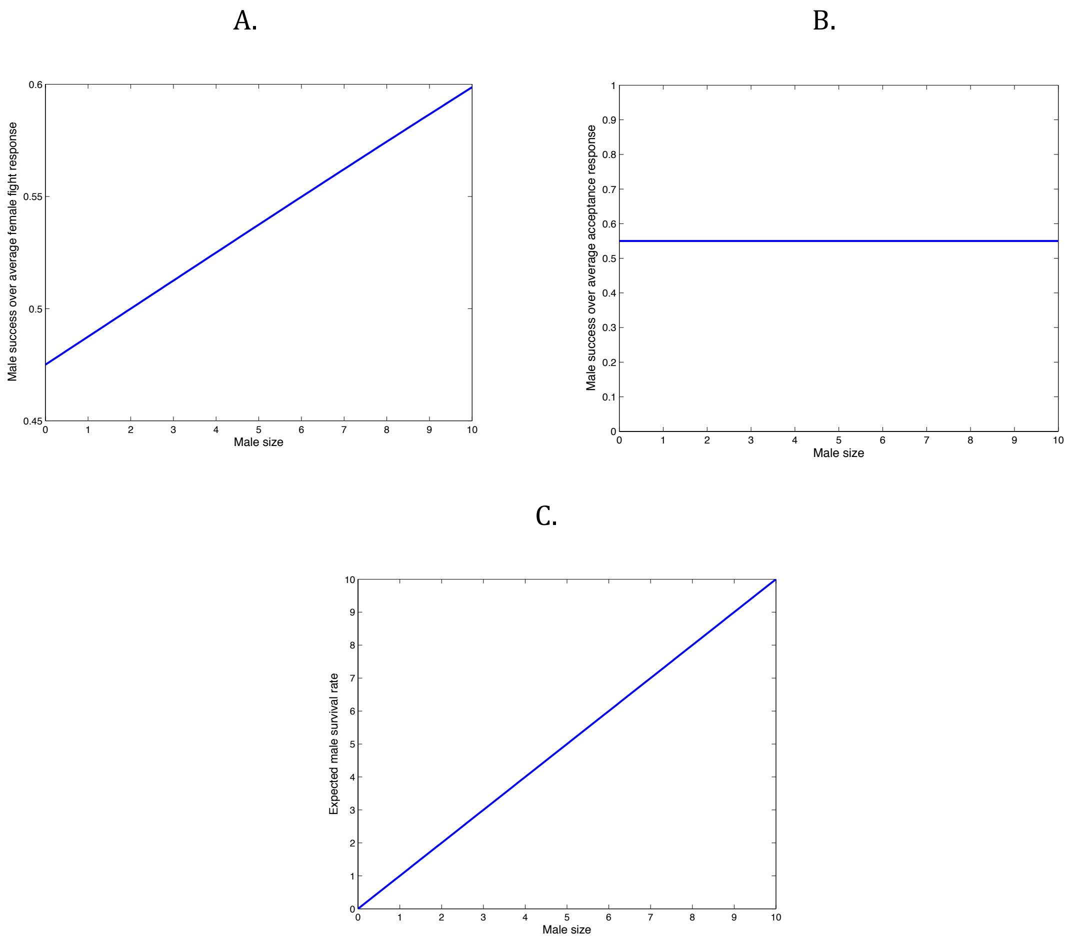

**Figure 4.4: The costs and benefits of large male size**

- **A.** **The female's high cost, high success response strategy is generally successful for avoiding copulation but success decreases as males become large.** Male success at securing a mating with a female who responds to his harassment with a high cost strategy is determined by his size; large males have an advantage. Here, example parameters are $c = 0.05$ and $f = 2$ to reflect empirical results (Grieve & Gilburn, unpublished data, 2011).
- **B.** **All males have an equal success rate at overcoming a female's low cost, low success response strategy.** A males ability to secure a mating with a female who uses a low cost strategy in response to his harassment is not related to his size. Here, the example uses $\gamma_A = 0.55$ and reflects empirical results (Blyth & Gilburn, unpublished data, 2011).
- **C.** **Large males are expected to survive longer.** The model assumes large size confers a survival advantage to males. Here it is assumed $a_1 = 0$ and $a_2 = 1$.

### 4.2.5 The Model

The convenience polyandry model consists of two fitness equations that allow antagonistic coevolution between the populations. Males evolve to optimise their body size according to their cost benefit trade-offs of size. Females evolve to optimise their response strategy according to their trade-off of survival costs versus reproductive benefits.

For both sexes fitness, $W$, is assumed to be a product of an individual's reproductive output per unit time, $R$, and their survival during that time, $S$.

$$W = Reprodution \times Survival$$

$$= R \times S$$

(Eqn 4.5)

#### *Male fitness*

Male fitness is modelled as:

$$W_M = R_M \times S_M$$

(Eqn 4.6)

Where

$$R_M = \alpha(1-\beta)\gamma_F + \alpha\beta\gamma_A$$

(Eqn 4.7)

and

$$S_M = a_1 + a_2 x$$

(Eqn 4.8)

The first term of the equation 4.7, $\alpha(1-\beta)\gamma_F$, gives the proportion of a males mating attempts greeted with a high cost response from the female but despite this he successfully coerces her and secures a copulation. The second term, $\alpha\beta\gamma_A$, gives the proportion of his mating attempts he receives a low cost response that ends in a copulation.

### Female fitness

Female survival decreases as her costs increase. This is very different to previous models, as none have considered costs to the female. Female fitness is:

$$W_F = R_F \times S_F$$

(Eqn 4.9)

Where $R_F$ is the reproductive output she receives due to her mating rate and $S_F$ is her survival. The female reproductive output, $R_F$, depends on the male mount rate, her response choice and how many copulations she endures. Female reproductive output is identical to male fitness.

$$R_F = \alpha(1-\beta)\gamma_F + \alpha\beta\gamma_A$$

(Eqn 4.10)

In the female fitness equation survival, $S_F$, is assumed to be determined by her costs, $C_F$. In reality the relationship between female costs, $C_F$, and female survival, $S_F$, is unknown. However considering the linearity of the effect mating costs had on female costs in the water strider study this model will assume that as costs for the female increase her survival decreases linearly.

$$S_F = 1 - \phi C_F$$

(Eqn 4.11)

The parameter $\phi$ is a scale factor; a large value of $\phi$ indicates that female survival is very susceptible to costs and small increases in costs can dramatically affect her survival.

The female cost is more complex as each response incurs some cost and each mount attempt she fails to deflect results in a copulation that also incurs a cost. Equation 4.12 shows how female costs are summed from the harassment attempts a female greets with a high cost response and avoids copulation, those she uses a high cost response and does not avoid copulating, those she uses a low cost response and avoids copulating and those she uses a low cost response and does not avoid copulating.

$$C_F = \alpha(1-\beta)\theta_F + \alpha(1-\beta)\gamma_F\mu + \alpha\beta\theta_A + \alpha\beta\gamma_A\mu$$

(Eqn 4.12)

### 4.2.6 Evolving the model

Having presented the model and detailed how the shape of functions were found to fit it to the Coelopids, I will now show how the model was used to explore antagonistic coevolution between mean male size, $x$, and female response, $\beta(x,T)$. Males can optimise their fitness by evolving their body size, $x$. Females can optimise their fitness by adjusting their threshold, $T$.

The fitness of the male and female populations are calculated using the fitness equations, $W_M$ and $W_F$ (equations 4.6 and 4.9). How the population evolves is calculated using the fitness gradient of the fitness curves at the mean male size, $\bar{x}$, and the mean female threshold, $\bar{T}$.

#### *Calculating the fitness gradient*

The fitness gradient of each fitness equation is calculated using the canonical equation, similar to the methods in Chapter 2 however now using a continuous time approach. The canonical equation applied to the fitness equations take the form:

$$\frac{d\bar{z}}{d\tau} = \frac{1}{2} r v^2 N \left.\frac{\partial W_i}{\partial z}\right|_{z=\bar{z}}$$

(Eqn 4.13)

Where $z$ is the target trait, either body size, $x$, in the males or response strategy threshold, $T$, in the females and $i$ denotes sex as appropriate. Parameter $\tau$ is long-term evolutionary time, parameter $r$ is the rate random mutations occur at, $N$ is the population size and $v^2$ is the genetic variance of the population which indicates the potential range of mutations that could occur (Abrams, 2001; Leimar, 2009; Dieckmann & Law, 1996). The constant $\vartheta$ can be used to replace $\frac{1}{2} r v^2 N$, similar to chapter two. The parameter $\vartheta$ is assumed to be 1 throughout, similar to chapter 2, because the interest is in where evolution will go not how long it will take to get there.

The canonical equation can then be shortened to:

$$\underbrace{\frac{d\bar{z}}{d\tau}}_{\substack{Change\ in\ trait\\ over\ time}} = \underbrace{\vartheta}_{Speed\ of\ evolution} \underbrace{\left.\frac{\partial W_i}{\partial z}\right|_{z=\bar{z}}}_{\substack{The\ fitness\ gradient\\ an\ individual\ with\\ trait\ z\ acheives}}$$

(Eqn 4.14)

Solving for $\frac{dz}{d\tau}$ in both fitness equations gives the change in trait over time. The male fitness gradient is found with:

$$\frac{d\bar{x}}{d\tau} = \vartheta \left.\frac{\partial W_M}{\partial x}\right|_{x=\bar{x}}$$

(Eqn 4.15)

The female fitness gradient is found with:

$$\frac{d\bar{T}}{d\tau} = \vartheta \left.\frac{\partial W_F}{\partial T}\right|_{T=\bar{T}}$$

(Eqn 4.16)

The full derivation of the partial derivatives, $\left.\frac{\partial W_M}{\partial x}\right|_{x=\bar{x}}$ and $\left.\frac{\partial W_F}{\partial T}\right|_{T=\bar{T}}$, is detailed in appendix 10.

### *Interpreting the fitness gradient*

At each time-step the fitness gradient of the mean male size $\hat{x}$, and the mean female threshold, $\hat{T}$, is calculated. The slope of this gradient determines how the population evolves. If:

| | |
|---|---|
| $\left.\frac{\partial W_i}{\partial z}\right|_{z=\bar{z}} > 0$ | The population should evolve a slightly larger value of trait *z* |
| $\left.\frac{\partial W_i}{\partial z}\right|_{z=\bar{z}} = 0$ | The population should not change its value of trait *z* because the population has reached a local fitness maxima |

$\left.\frac{\partial W_i}{\partial z}\right|_{z=\bar{z}} < 0$ The population should evolve a slightly smaller value of trait $z$

### *Using the fitness gradient to simulate evolution*

A stochastic program was built in MatLab utilising differential equation solver function ‘ode15s’ that would evaluate the fitness gradient of both populations at each time step. This solver is useful because it chooses the size of each time step depending on the fitness gradient; if the gradient is steep the time step is small if it is shallow the time step is large. This allows for much faster calculation of equilibrium for a complex system because it allows the program to ‘skip’ areas where very little change occurs. Running the program with the fitness equations over many time steps allowed antagonistic coevolution to be simulated.

The general assumptions of evolution here are similar to those stated in chapter 2, however the method of evolution differs slightly. Here the use of ‘ode15s’ means the value and sign of the fitness gradient determine the speed of evolution. This is in contrast to chapter 2 where the speed of evolution was constant and stepped at $\pm 1$ day for mean arrival and $\pm 0.1$ standard deviations for distribution width of arrival dates. The main difference between modelling evolution here and in chapter 2 is that here evolution follows continuous time, whereas in chapter 2 evolution occurred discretely over each generation. In chapter 2 a discrete approach was taken with migration as an annual event, here time and reproduction are continuous so a continuous approach is used.

### 4.2.7 Analysing the model

As detailed this model has been built using real data as much as possible and the functions, parameters and their sources are summarised in table 4.1. These original parameter values make the baseline parameter set.

#### *Exploring the baseline parameter set*

First the model was tested using only the baseline parameter set. From these values it was run until it reached equilibrium at approximately $10^7$ time units. The values that male size and female threshold evolved and stabilised on were recorded. Before these values could be assumed to be indicative of an equilibrium the initial conditions of the evolvable traits, $x$ and $T$, were tested for their sensitivity. The parameter $x$ was tested over an initial value ranging from 0.001 to 10 and always evolved to the same point. The parameter $T$ was tested over a range of initial values from -10 to 15 and always evolved to the same point. Further values out with this range were not tested because they were deemed biologically irrelevant.

#### *Sensitivity analysis*

Following identification of the evolutionary tract the baseline parameter set followed each individual parameter was tested over a range of values to identify its effect on the model and hence its role in the evolution of convenience polyandry.

#### *Interpreting the output*

The output of each sensitivity analysis test plots the final values of $x$ and $T$ the populations evolve to under each tested parameter value. How this effects the evolution of convenience polyandry can appear difficult to interpret however so the range of the male population and the range of the mixed strategy part of the female response curve (over the slope of the sigmoid) are estimated on each plot using a truncation method. Note the use of truncation is for ease of explanation of output only and is not integral to the model design.

Male size was assumed to be normally distributed throughout the populations and to create obvious boundaries at the upper and lower limits of male size a 90% confidence interval was employed; male distribution is cut-off at the upper and lower 5% of sizes in the normal distribution. The upper limit of the male distribution used is given by:

$$x_{Up} = x + 1.645\sigma$$

(Eqn 4.19)

And the lower by:

$$x_{Low} = x - 1.645\sigma$$

(Eqn 4.20)

Where $Z = 1.93$ from the standard normal tables and $\sigma = 0.8$. This allowed the final upper and lower limit of male size for each parameter value to be plotted.

The mixed strategy area of the sigmoidal $\beta(x, T)$ curve is important in determining the presence or absence of convenience polyandry. To create visual boundaries of this area it was assumed males whose size caused them to receive less than a 10% probability of receiving a low cost response always received a high cost response and males whose size caused them to receive a greater than 90% probability of receiving an low response always received a low cost response.

The lower boundary of the mixed strategy area of the $\beta(x, T)$ curve was determined by:

$$\beta_{Low} = -ln\left(\frac{1}{0.1} - 1\right) - T$$

(Eqn 4.17)

The upper boundary of the $\beta(x,T)$ curve was determined by:

$$\beta_{Up} = -ln\left(\frac{1}{0.1} - 1\right) + T$$

(Eqn 4.18)

These are derived similarly to the length of time season in Chapter 2 a full explanation of which is detailed in appendix 3.

The bands of male size distribution and female mixed strategy area are indicated on the plots by shading. Convenience polyandry was determined to occur if the male distribution of sizes overlapped the mixed strategy area of the $\beta(x,T)$ curve. If the male population band is above the convenience polyandry band the female population exhibits a singular strategy of use a low cost, low success response against all males for those parameter values. If the male population band is below the convenience polyandry band the female population exhibits a singular strategy of use a high cost, high success response against all males for those parameter values.

**Table 4.1 Summary of model functions, parameters and their empirical sources.** Each function is summarised by its respective parameters and the empirical sources of the baseline parameters are detailed where appropriate.

| Function | | Parameters | Base line value | Source |
|---|---|---|---|---|
| Male mating rate | $\alpha(x)$ | $a$<br>$b$ | 1.68<br>3 | Empirical data on Coelopid male willingness to mate (Dunn et al. 1999) |
| Female response strategy | $\beta(x,T)$ | $s$<br>$T(0)$<br>$x(0)$ | 1.32<br>4.5<br>5.409 | Empirical data on Coelopid female strategy choice and average male size (Blyth & Gilburn, 2011) |
| Female high cost response fee | $\theta_F$ | $j$<br>$k$ | 1.25<br>1 | Linear shape of function derived from study of water strider metabolism during mating (Watson et al. 1998) |
| Female low cost response fee | $\theta_A$ | $\theta_A$ | 0.5 | Estimate |
| Female copulation fee | $\mu$ | $\mu$ | 20 | Estimate |
| Male success over high cost response | $\gamma_F(x)$ | $c$<br>$f$ | 0.05<br>2 | Empirical data on male mating success and size (Grieve & Gilburn unpublished data, 2011) |
| Male success over low cost response | $\gamma_A(x)$ | $\gamma_A(x)$ | 0.55 | Empirical data on Coelopid female strategy choice and average male size (Blyth & Gilburn, 2011) |
| Reproduction and survival scale parameter | $\phi$ | $\phi$ | 0.1 | Estimate |
| Male survival | $S_M$ | $a_1$<br>$a_2$ | 0<br>1 | Estimate<br>Estimate |

## 4.3 Results part 1: The baseline parameters

Initially the model was run with all the parameters gathered from the data (summarised in Table 4.1). Male size evolved quite rapidly to a stable size that was much smaller than the mean size value used as the initial size. Initial male size was 5.409 and final male size was 2.36 (figure 4.5a). Female threshold was still decreasing after 1000 generations but on a much longer time scale of $10^6$ generations this decrease had markedly slowed. Further simulations showed $T \rightarrow -7$ after $10^6$ generations (figure 4.5b). At this point the system has not reached equilibrium but further generations show only further decreases in $T$ which does not affect the final conclusions. The models failure to go to equilibrium is a reflection of the limitation of the sigmoidal curve used for $\beta(x, T)$; at extreme ends of the sigmoidal curve $\beta(x, T)$ is never equal to zero. Using a time cut off of $10^6$ generations provided sufficient time for conclusions on the evolutionary trajectories of all simulations to be drawn and biological relevance to be maintained. Further generations did not affect the outcome of the models in regards to absence or persistence of convenience polyandry.

The initial male size and female response gathered from the data is illustrated in figure 4.6c along with the final male size and female response after the model was run for $10^6$ generations. The final values show no overlap between male size distribution and the mixed strategy area of the female distribution curve so demonstrates convenience polyandry is selected out of the female response and the female population eventually evolves to adopt a singular strategy of use a low cost response against males of all sizes.

These initial results indicate that at the baseline values drawn from real data, convenience polyandry should rapidly be selected against. A number of possible reasons for this are explored in the discussion but one of these reasons is that some of the chosen parameters may be inappropriate, particularly those that were estimated, and this is where the sensitivity analysis in part 2 of the results becomes important.

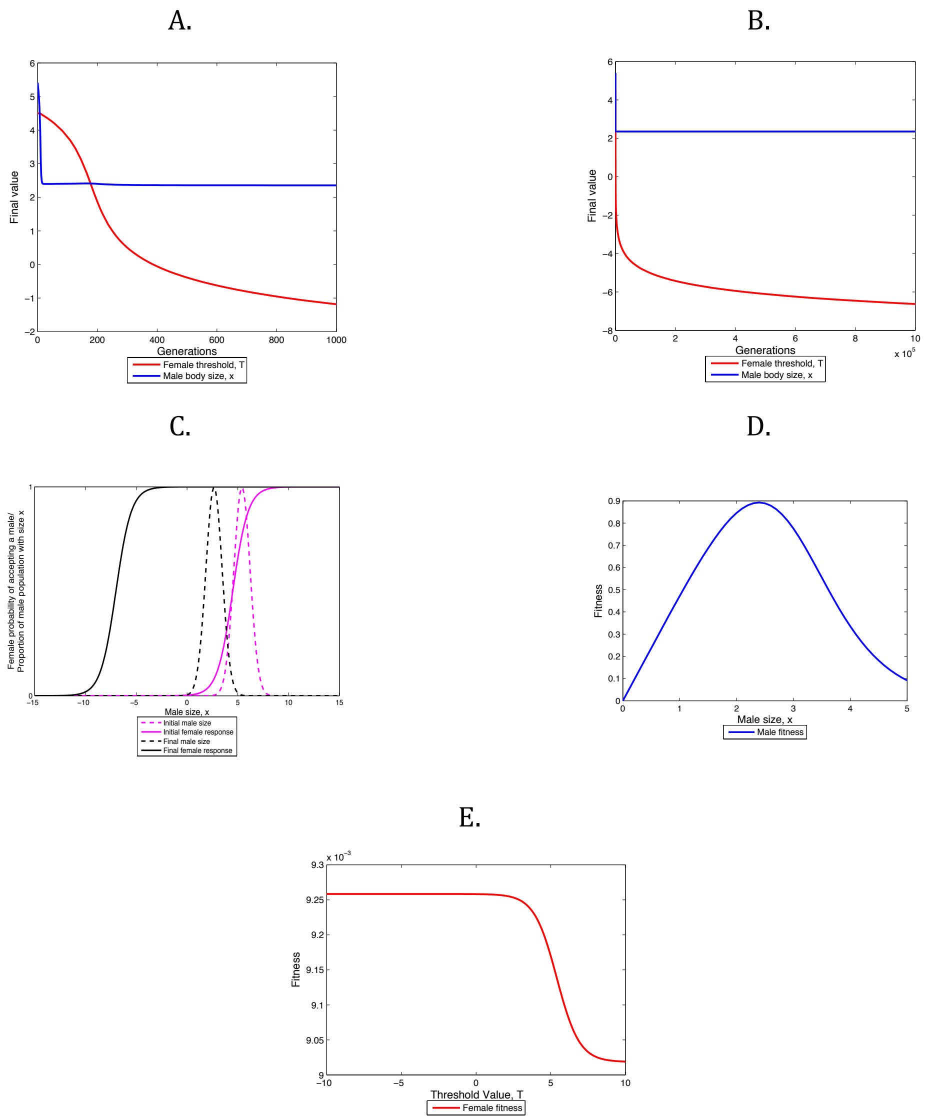

**Figure 4.5: The evolutionary trajectory of the baseline parameters**

A. **1000 time steps is not long enough to reach stability for the baseline parameters.** Parameters were set as follows; $a = 1.68, b = 3, j = 1.25, k = 1, c = 0.05, f = 2, \theta_A = 0.5, \gamma_A = 0.55, \mu = 20$ and $s = 1.32$. Initial male size was $x(0) = 5.409$ and initial female threshold was $T(0) = 4.5$. After 1000 generations male size stabilized at approximately $x = 2.36$. Female threshold reached $T = -1.18$ and was still slightly decreasing.

B. **The baseline parameters reach stability by $10^6$ time steps.** After $10^6$ generations female threshold was still ever so slightly decreasing but at $10^6$ generations $T \rightarrow -7$.

C. **Initial and final male size and female response.** The final values show the entire male population should receive an low cost response indicating pre-mating struggles and convenience polyandry are being selected against.

D. **Male fitness curve at final iteration.** This illustrates the fitness curve the male population achieves on the $10^6$ th time step of the model; it shows a peak of fitness at approximately $x = 2.36$ where the model shows male size evolves to.

E. **Female fitness curve at final iteration.** This illustrates the fitness curve the female population achieves on the $10^6$ th time step of the model; it shows female fitness is maximised with approximately $T < 1$.

## 4.4 Results part 2: Sensitivity analysis

### 4.4.1 Male mating rate, $\alpha(x)$

#### *The gradient of the $\alpha(x)$ curve, a*

The model is tested over values of $a$ ranging between 0.2 and 10. When $a = 0.2$ the slope of $\alpha(x)$ is shallow and male size has little effect on mating rate; when when $a = 2$ the slope of $\alpha(x)$ is steep and male size has a large effect on mating rate (figure 4.6a)

The sensitivity analysis shows manipulating $a$ does not affect the evolution of convenience polyandry; for all values of $a$ female adopt a singular strategy of a low cost response against males of all sizes. There is a very slight overlap in male distribution and female mixed strategy area when $0.4 < a < 1.4$ but the effect is minimal as for even the smallest males the probability she will use a high cost response is small. At low values of $a$ male size is larger than the control (when $a = 0.2$, $x = 7.17$) and as $a$ increases male size decreases. At low values of $a$ female threshold is higher than the control (when $a = 0.2$, $T = 2.396$) and as $a$ increases female threshold decreases (figure 4.6b).

#### *The midpoint of the $\alpha(x)$ curve, b*

The model is tested over values of $b$ ranging between -5 and 10. When $b = 0$ males of all sizes in the population are unwilling to mate and the average mating rate is almost nil, when $b = 10$ all males are very willing to mate (figure 4.6c). Note that male willingness to mate curve must be considered in conjunction with the male distribution of size; when $b$ is very low it indicates no male in the population is particularly willing to mate and when it is high all males mate at a very high rate. Only when the mating rate curve overlaps the distribution is there variation in mating rate within the population.

The results show that manipulating $b$ affects the evolution of convenience polyandry and female strategy for low values of $b$. When $b < 3$ convenience polyandry evolves, illustrated by overlap between the mixed strategy band and the male size distribution. When $b > 3$ a singular strategy of a low cost response against all males evolves. As $b$ increases mean male size increases (figure 4.6d).

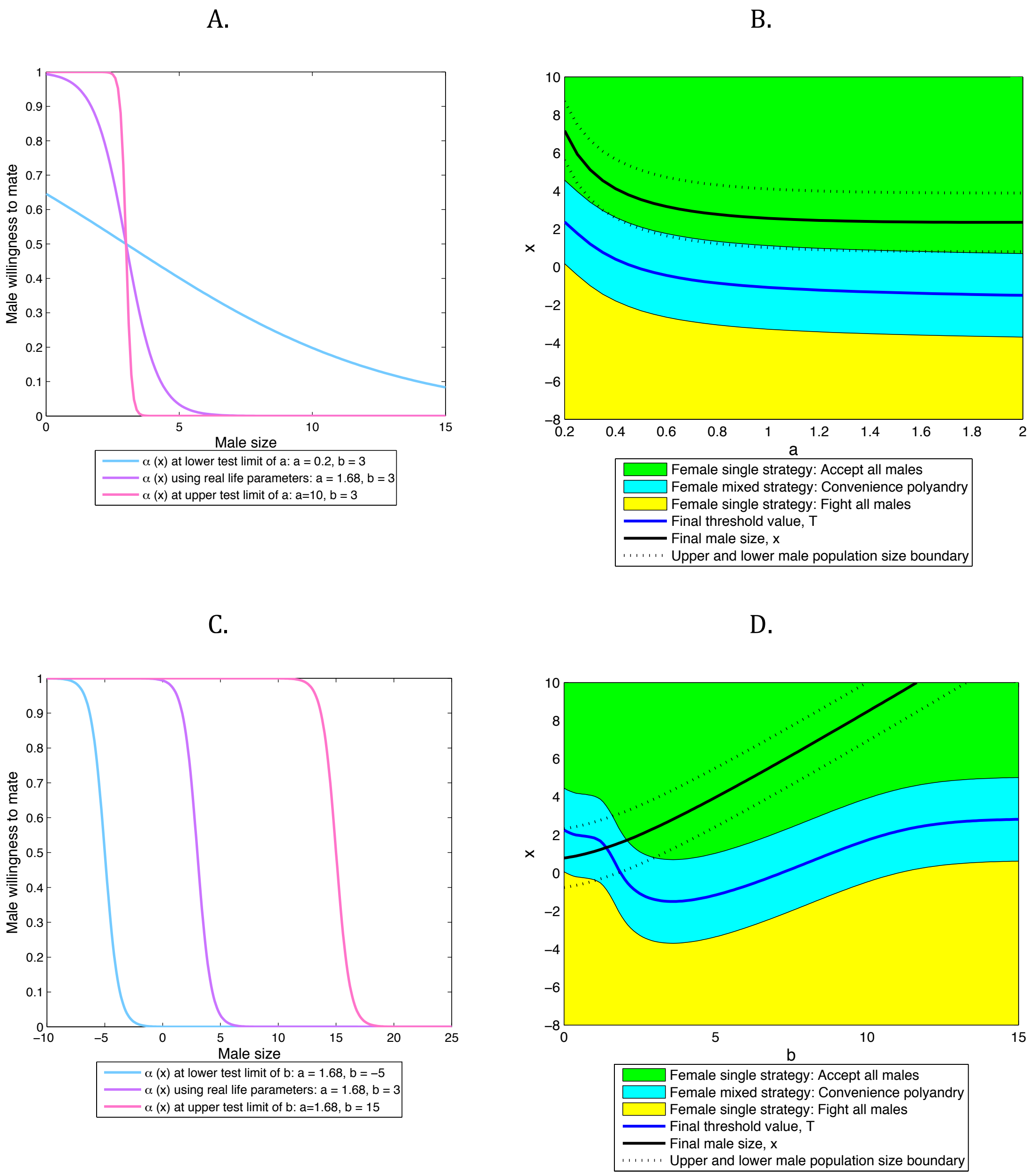

**Figure 4.6: Sensitivity analysis of male mating rate $\alpha(x)$.**

- **A. Examples of $\alpha(x)$ at the upper and lower test limits of $a$.** The model is tested over values of $a$ ranging between 0.2 and 10.
- **B. The effect of varying $a$ on male size and female threshold.** The parameter $a$ has very little role in the evolution of convenience polyandry.
- **C. Examples of $\alpha(x)$ at the upper and lower test limits of $b$.** The model is tested over values of $b$ ranging between -5 and 10.
- **D. The effect of varying $b$ on male size and female threshold.** The parameter $b$ has a role in the evolution of convenience polyandry.

### 4.4.2 Female high cost, high success response strategy fee, $\theta_F$

#### *The gradient of the $\theta_F$ curve, j*

The model is tested over values of $j$ ranging between 0 and 5. When $j = 0$ a female's high cost response fee is constant across all male sizes. When $j = 5$ large males are much more expensive to resist than small ones; there is high variation in the costs of a high cost response across males within the population (figure 4.7a). Manipulating $j$ affects the evolution of convenience polyandry. When $j < 1.25$ convenience polyandry evolves, illustrated by overlap between the mixed strategy band and the male size distribution. When $j > 1.25$ a singular strategy of a low cost response against all males evolves (figure 4.7b).

#### *The midpoint of the $\theta_F$ curve, k*

The model is tested over values of $k$ ranging between -5 and 15; increasing $k$ increases the cost for a female of using a high cost response against males of all sizes (figure 4.7c). Manipulating $k$ affects the evolution of convenience polyandry. When $-3 < k < 1$ convenience polyandry evolves. When $k < -3$ females evolve a singular strategy of a high cost response against all males. When $k > 1$ females evolve a singular strategy of a low cost response against all males (figure 4.7d).

#### *Summary of the effect of costs of female high cost, high success response strategy fee, $\theta_F$*

In summary variation throughout the male population of the female fee for using of a high cost strategy affects the evolution of female strategy. Convenience polyandry evolves when the success rate of a high cost response is lower than the success rate of a low cost response for small males but higher for large males.

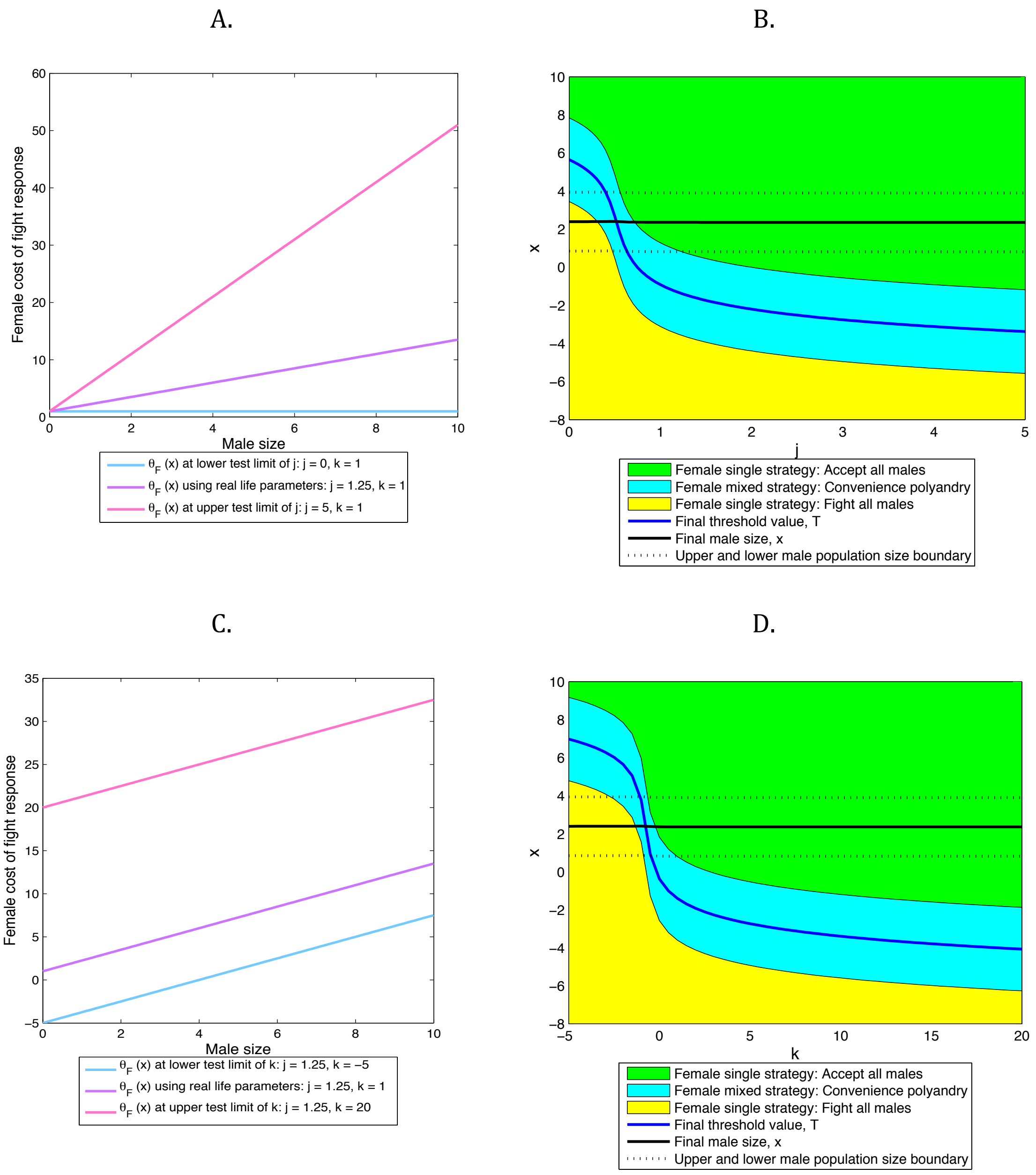

**Figure 4.7: Sensitivity analysis of the function of female high cost response fee, $\theta_F$**

- **A. Examples of $\theta_F$ at the upper and lower test limits of *j*.** The model is tested over values of *j* ranging between 0 and 5.
- **B. The effect of varying *j* on male size and female threshold.** The parameter *j* has a role in the evolution of convenience polyandry.
- **C. Examples of $\theta_F$ at the upper and lower test limits of *k*.** The model is tested over values of *k* ranging between -5 and 15.
- **D. The effect of varying *k* on male size and female threshold.** The parameter *k* has a role in the evolution of convenience polyandry.

### 4.4.3 Female low cost, low success response strategy fee, $\theta_A$

The model is tested over values of $\theta_A$ ranging between 0 and 10. When $\theta_A = 0$, the females receive no fee for using this response. Manipulating $\theta_A$ affects the evolution of convenience polyandry and female strategy. Changing the female cost of a 'low cost response' has no effect on male size. Convenience polyandry evolves when $0.4 < \theta_A < 4.1$, illustrated by overlap between the mixed strategy band and the male size distribution (figure 4.8). When $\theta_A < 0.4$ a singular strategy of use 'low cost response against all males' evolves. When $\theta_A > 4.1$ a singular strategy of use a high cost response against all males evolves.

In summary when the low cost response fee is low females choose to only use the low cost response, as the fee increases convenience polyandry evolves.

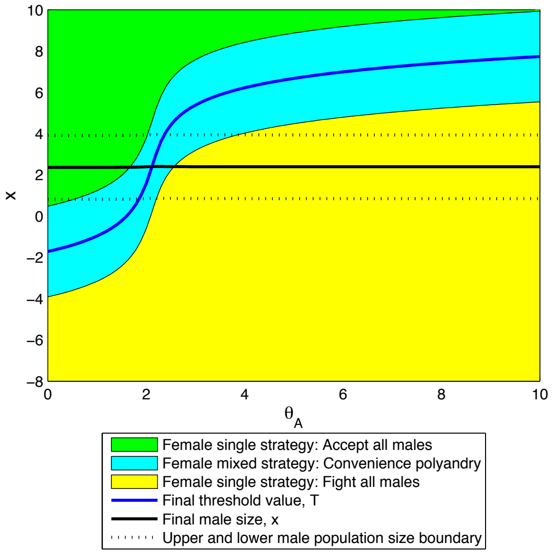

**Figure 4.8: Sensitivity analysis of the female low cost response fee, $\theta_A$**
The model is tested over values of $\theta_A$ ranging between 0 and 10 and shows that $\theta_A$ has a role in the evolution of convenience polyandry.

### 4.4.4 Female cost of copulation, $\mu$

The model is tested over values of $\mu$ ranging between 0 and 100. When $\mu = 0$, copulation has no cost.

The sensitivity analysis shows manipulating $\mu$ affects the evolution of convenience polyandry and female strategy. When $30 < \mu < 67.5$, convenience polyandry occurs. This is illustrated by the overlap in male distribution and female mixed strategy bands (figure 4.9). When $\mu < 30$, a singular strategy of use a 'low cost response against all males' evolves. When $\mu > 67.5$, a singular strategy of use a 'high cost response against all males' evolves. In summary copulation fee increases the more incentive the female has to avoid copulating and she will use the most effective means to reduce her total costs.

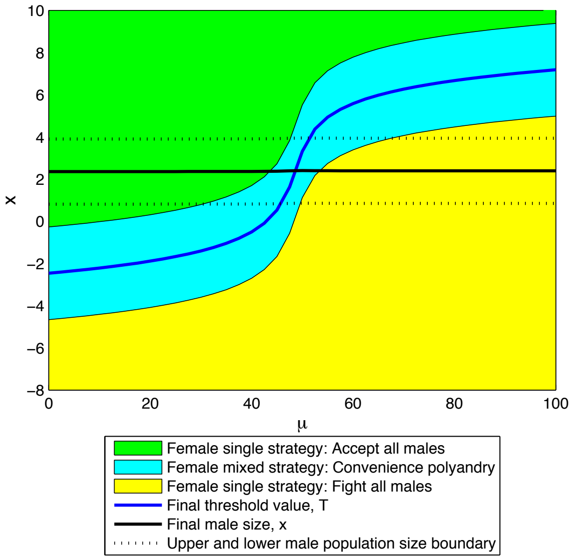

**Figure 4.9: Sensitivity analysis of the effect of the female copulation fee**
At low values of $\mu$ females use a low cost response against all males, at high values of $\mu$ females use a high cost response against all males. The parameter $\mu$ has a role in the evolution of convenience polyandry.

### 4.4.5 Male success rate over female high cost response strategy, $\gamma_F$

#### *The gradient of the $\gamma_F$ curve, c*

The model is tested over values of $c$ ranging between 0 and 10 which increases the slope of the male success over female high cost response function from flat to steeply sigmoidal. The parameter $c$ gives the importance of male size on success; a low $c$ and male size has very little effect on success over a female high cost response. With a high $c$ value small males are very poor at overcoming a high cost response and large males are very successful at overcoming a high cost response (figure 4.11a).

The sensitivity analysis shows manipulating $c$ has no role in the evolution of convenience polyandry. Increasing the steepness of the success curve cause the female threshold to decrease but this is already so low it does not cause a change in female strategy (figure 4.11b). When $c$ is tested using different values of $f$ it shows $c$ has no effect on whatever strategy evolves.

#### *The midpoint of the $\gamma_F$ curve, f*

The model is tested over values of $f$ ranging between -80 and 40. Care must be taken when interpreting $f$ because as $f$ increases the males become less successful at overcoming a high cost response from a female (figure 4.11c). Note that when $f \approx 2$ there is overlap between the success of a high cost response and the success of a low cost response (baseline parameter $\gamma_A = 0.55$).

Manipulating $f$ has an effect on the evolution of convenience polyandry (figure 4.11d). Convenience polyandry occurs when $2 < f < 12$ and $f > 23$. When $f < 2$ a singular strategy of use a 'low cost response against all males' evolves and when $12 < f < 23$ a singular strategy of use a 'high cost response against all males evolves'.

#### *Summary of the effect of male success over female high cost response strategy, $\gamma_F$*

In summary the variation of male success over a female high cost response within a population has very little effect on the evolution of female strategy but the average success rate does. When the males coerce copulations from a high cost response at a higher rate than over a low cost response the females do not use a high cost response. When females can use a high cost response to easily avoid copulation they do. Convenience polyandry evolves only over a narrow band of $f$.

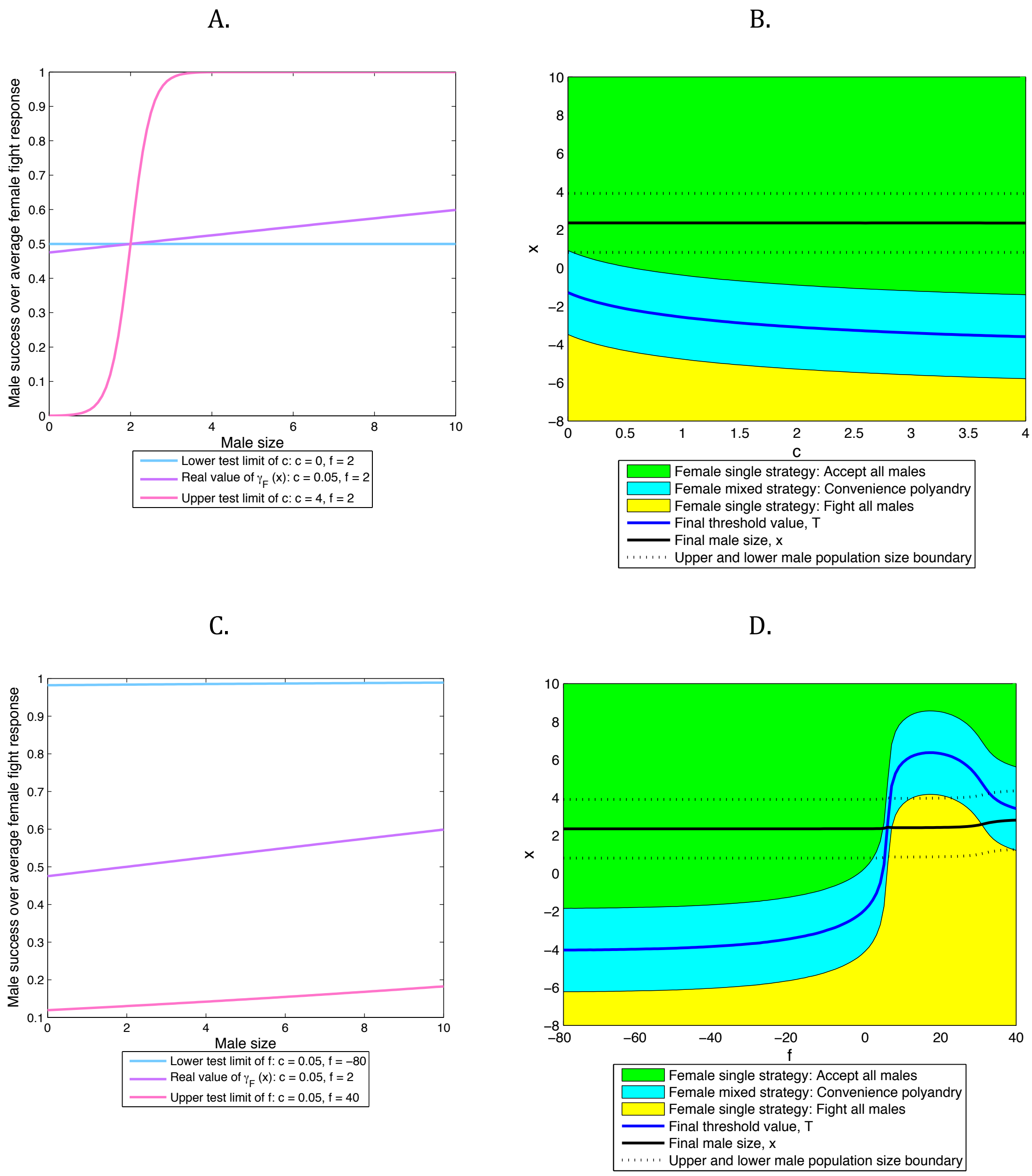

**Figure 4.10: Sensitivity analysis of the effect of male success over female high cost response, $\gamma_F$**

- **A. Examples of $\gamma_F$ at the upper and lower test limits of $c$.** The model is tested over values of $c$ ranging between 0 and 10.
- **B. The effect of varying $c$ on male size and female threshold.** The parameter $c$ has no role in the evolution of convenience polyandry
- **C. Examples of $\gamma_F$ at the upper and lower test limits of $f$.** The model is tested over values of $f$ ranging between 0 and 10.
- **D. The effect of varying $f$ on male size and female threshold.** The parameter $f$ has a role in the evolution of convenience polyandry

### 4.4.6 Male success rate over female low cost response strategy, $\gamma_A$

The model is tested over a range of $\gamma_A$ values from 0 to 1. When $\gamma_A = 0$ using the low cost response guarantees the female will receive a copulation.

The sensitivity analysis shows manipulating the value of $\gamma_A$ has an effect on the evolution of convenience polyandry. When $0.55 < \gamma_A < 0.635$ convenience polyandry evolves (figure 4.12). Also when $\gamma_A < 0.185$ convenience polyandry evolves, this is likely because when $\gamma_A < 0.185$ male size evolves to be slightly smaller than usual.

In summary when a low cost response is more likely to result in copulation than a high cost response it is used regularly. When it becomes less effective than a high cost response it is used less regularly.

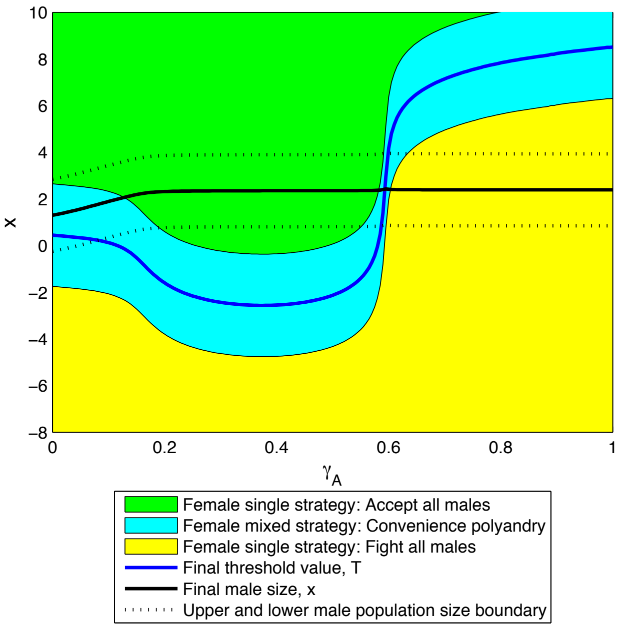

**Figure 4.11: Sensitivity analysis of the effect of male success over female low cost response, $\gamma_A$**

Low values of $\gamma_A$ can cause convenience polyandry to evolve. The parameter $\gamma_A$ has a role in the evolution of convenience polyandry.

### 4.4.7 Female survival and reproduction scalar

The model is tested over a range of $\phi$ between 0 and 1. This modifies the relative importance of fitness due to reproductive benefits, $R_F$, and decreasing fitness due to survival costs, $S_F$, on overall fitness, $W_F$, as detailed in equation 4.11. When $\phi = 0$ female fitness is determined solely by reproductive benefits from securing matings that will lead to offspring production; she receives no costs of mating. When $\phi > 0$ female fitness is determined by a trade-off between benefits gained through reproduction and costs incurred through mating. As $\phi \rightarrow 1$ the relative weighting of the importance of the costs she incurs increases.

The sensitivity analysis shows $\phi$ did not change the final evolutionary strategy of the population. Varying $\phi$ between 0 and 1 had no effect on the evolutionary trajectory of the population using the baseline parameters. When $\phi$ is very close to zero convenience polyandry may evolve but only with the females using a high cost response against the very smallest males (figure 4.12). Increasing $\phi$ caused the female threshold to decrease; this reflects that as the detrimental effect of costs on female survival increases her likelihood of adopting convenience polyandry of a high cost response decreases. In reality though the threshold is already so far below male size this has no noticeable effect.

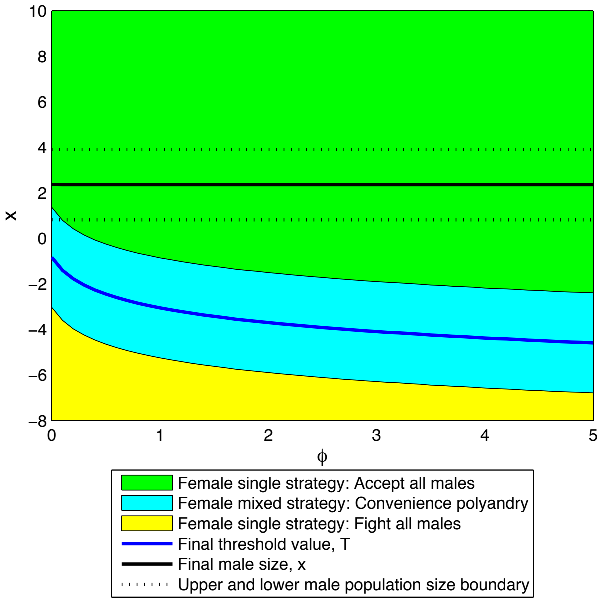

**Figure 4.12: Sensitivity analysis of the scale parameter $\phi$.**
The parameter $\phi$ has very little role in the evolution of convenience polyandry.

## 4.5 Discussion

This work introduced the first model of convenience polyandry. It developed existing models of sexually antagonistic coevolution by reconstructing them to include female costs of mating as an important driver in female strategy evolution (Gavrilets *et al.* 2001; Rowe *et al.* 2005; Hoyle & Gilburn, 2010). Each individual parameter in the model was examined in a sensitivity analysis to determine its role in the evolution of convenience polyandry in the model. The parameters shown to have the largest effects of female strategy evolution are the costs and success of high and low cost response strategies.

The model provides support for the theory of convenience polyandry; when copulation is expensive females may use a mixture of response strategies to avoid matings and minimise her costs (Thornhill & Alcock 1983). The models show that a narrow range of conditions are required for convenience polyandry to evolve and the probability of achieving these conditions is low; this explains why so few species which exhibit male coercion show convenience polyandry. The model predicts that if there is variation in the cost of strategies against males in the population convenience polyandry is likely to evolve. This means convenience polyandry is most likely to evolve when the coefficient of variation of male harassment traits is large.

### 4.5.1 Convenience polyandry evolves under a very narrow parameter range

The results of the model show that convenience polyandry only occurs over a narrow range of parameters (figure 4.13). Although convenience polyandry is recorded in a wide range of unrelated species the actual number of species that exhibit convenience polyandry is relatively low. If the conditions required to evolve convenience polyandry are very specific this could explain why although the range of species is diverse the total number of species that exhibit convenience polyandry appears low. The model shows the evolution of a singular response to male harassment is much more common than the evolution of convenience polyandry.

What are the conditions necessary for convenience polyandry to evolve? One condition that may cause convenience polyandry to evolve is if the costs of a struggle are greater than the costs of the alternative strategy for some males and vice versa for other males (figures 4.7d and 4.8). This is likely to occur when there is high variation in the coefficient for male harassment traits because a high variation in harassment trait means there will be high variation in the cost of resistance. This is particularly relevant in the coelopids because they show a very large variation in male size and a large variation in ability to overcome female resistance as a result. A meta-analysis into the other studies that exhibit convenience polyandry would be useful to identify the role of variation in male harassment trait and correlation with incidence of convenience polyandry.

Another condition that could cause convenience polyandry to evolve is if the costs of each strategy are similar (figure 4.6d), or the cost of a copulation is high. The cost of copulation plays an important role in strategy evolution because it affects the incentive for the female to reduce her costs; when copulation is cheap she can use a low cost, low success resistance strategy but as the costs increase she must use a high cost but high success strategy more often to avoid copulation (figure 4.9). A further condition that may cause convenience polyandry to evolve is if both strategies have similar success rates at preventing males from copulating (figures 4.10d and 4.11), or there exists a large coefficient of variation in mating rate within the population (figure 4.6d).

To evolve the singular strategy of using a low cost response against all males requires male mating rate to be very high (figure 4.6d), the ‘high cost, high success’ response strategy fee must be much higher than the ‘low cost, low success response’ strategy fee (figure 4.7d) or the low cost response strategy must be more successful at deterring males than the high cost response strategy. A ‘low cost, low success strategy’ may also evolve as the singular strategy if the cost of copulation is low because then the female benefits from multiple matings with very little decrease in survival. A singular strategy of use a ‘high cost, high success response' against all males will also evolve if the cost of copulation is extremely high (figure 4.9). This is because each copulation has a very large effect on female survival. A high cost strategy is likely to evolve as the singular strategy if it is particularly successful at deterring male from copulating, or the alternative strategy response is particularly poor at deterring males from copulating (figure 4.10d and 4.11).

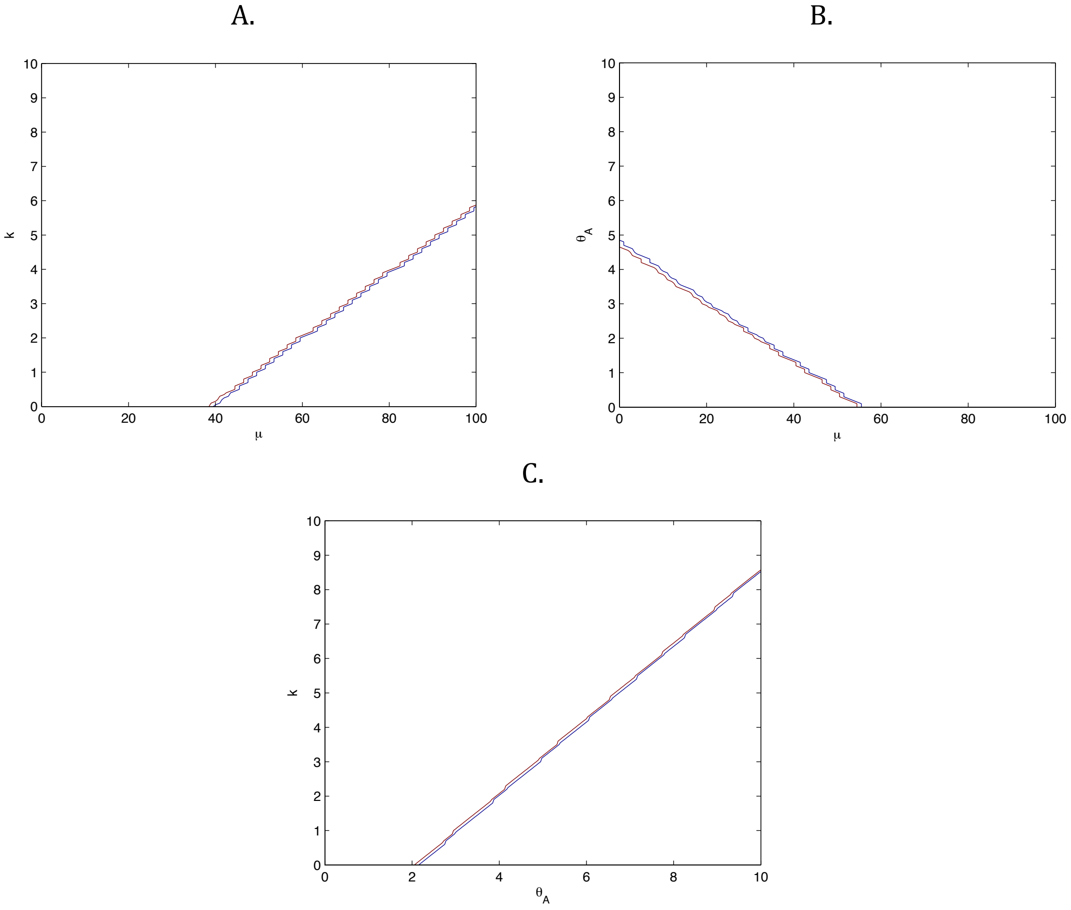

**Figure 4.13: Convenience polyandry evolves over a narrow band of parameters.**

A. **Copulation fee, $\mu$, versus female high cost response strategy fee, $k$.** The area within the narrow band in each plot indicates the value for each respective strategy or copulation fee convenience polyandry will evolve.
B. **Copulation fee, $\mu$, versus female low cost response strategy fee, $\theta_A$.**
C. **Female high cost response strategy fee, $k$ versus female low cost response strategy fee, $\theta_A$.**

### 4.5.2 Optimal male and female trait values exist but these do not often show convenience polyandry

The model shows there exists a stable optimal male size and optimal female threshold value. This was initially demonstrated in the baseline model which showed given the baseline parameters male and female size and threshold would evolve to a stable, biologically realistic optimum point. The finding of an optimum point is in contrast to previous modelling studies which predicted that sexually antagonistic coevolution can result in a continuous escalation of traits under sexual conflict, an 'arms race,' where a trait in one sex evolves rapidly to extreme values in response to evolution of a response trait in the opposite sex (Gavrilets et al, 2001; Rowe et al, 2005). This is likely because in the model presented here, reproduction and survival are more directly linked as a multiplicative rate (equation 4.5) compared with two additive terms of natural and sexual selection in both Gavrilets et al, (2001) and Rowe et al, (2005). The model here also includes an important selection pressure against escalation of male size; willingness to mate.

The baseline parameters show the populations to tend to optimal values however these values do not show convenience polyandry. The model shows rapid evolution of the males to a smaller optimal size and gradual decrease of the female response threshold. Female threshold decreases so far below mean male size that convenience polyandry is selected out of the population fairly quickly and replaced with a singular strategy of using a low cost response against all males (figure 4.6). This further indicates the narrow range of parameters required for convenience polyandry to evolve and supports the idea that the low number of species that exhibit convenience polyandry is because few have the conditions within the range for it to evolve. Convenience polyandry could be a transitory phase in evolution between the female switching from one singular strategy to the other. If this is the case, this makes an interesting research question because so far no studies exist to see if convenience polyandry does get selected out of a population in the long term.

Some assumptions of the model such as the effect of male size on male survival were estimated. Other parameters estimated included the costs of the low cost response, $\theta_A$ and the cost of copulation, $\mu$,. The parameters of $j$ and $k$ of the high cost response fee were also estimated but the shape of the high cost response fee function they made up, $\theta_F$, was drawn from empirical evidence (Watson et al. 1998). The model was designed such that exact values of parameter were less important than the shape of functions and balance between them. It would be interesting to retest the model using data on the costs of strategies and mating from other species that exhibit convenience polyandry. It would also be particularly interesting to understand how the cost of copulation balances against the costs of each resistance strategies and does harassment trait influence male survival in species that exhibit convenience polyandry. Unfortunately empirically estimating the costs of mating and separating the costs of mating from the costs of harassment is incredibly difficult.

Another assumption that would be interesting to explore is the effect of cost on female survival. Here it was assumed that as female costs increased, female survival, and thus length of time where she could reproduce, decreased linearly (eqn 4.11). For a long time this has been assumed to be the case and some of the commonly used methods of measuring sexual selection rely on this assumption (Andersson & Iwasa, 1996). The Bateman gradient for example is a regression between the number of matings an individual achieves in its life and the number of viable offspring it produces. If this gradient is steep, the number of mates has a large effect on number of offspring and thus sexual selection acts strongly and mating is costly. The Bateman gradient is used widely as a standardised measure of the costs of mating that is comparable between species but relies on the assumption that this relationship is linear (Andersson & Iwasa, 1996; Jones et al. 2000; Kokko et al. 2012; Fritzsche & Arnqvist, 2013). Recently empirical studies have indicated that the relationship between female costs and fitness or survival is nonlinear. Some studies indicate there is an optimal mating rate up to which multiple mating increases a female's fitness but beyond which decreases her fitness as the costs of mating outweigh the benefits (Arnqvist & Nilsson, 2000; Ronkainen et al. 2010; Honkola et al. 2011). There is as yet no evidence of the exact shapes of the decreasing relationship between female costs and survival in species that exhibit convenience polyandry so a linear form was chosen here to retain mathematical simplicity in an already complex model. For future work however it would be interesting to both test the model assuming different shaped functions of cost and survival and also to find empirical evidence that could clarify the shape of the relationship in species that exhibit convenience polyandry.

### 4.5.3 Female threshold is more sensitive to parameters than male size

The results of the model suggest that the female optimum threshold is much more sensitive to changes in parameters than male optimum size. Female threshold was affected by almost all parameters whereas male optimal size was shown to be affected by their mating rate or willingness to mate, through both parameters $a$ and $b$. Male populations would optimise their size to maximise their mating rate. The optimal size is small enough to keep a strong mating rate but large enough to overcome many female's resistance response. No other parameter significantly affected male size like the male mating rate indicating male size is driven primarily by sexual selection. It is widely theorised that male fitness is maximised when their mating rate is maximised and these results support this (Arnqvist & Nilsson, 2000). An interesting point this raises is that it could suggest females drive the fitness of the entire population. If males evolve to simply maximise the number of successful matings they achieve then it is female response and evolution of strategy that determines how many successful matings in the population actually occur; if females control this total then they control the fitness of the entire population.

### 4.5.5 Conclusion

Combining the results of the eradication of convenience polyandry from the baseline parameters with the finding from the sensitivity analysis that convenience polyandry should only evolve over a very specific range of parameters it seems unlikely that convenience polyandry will evolve very regularly. It also seems unlikely that convenience polyandry should persist long term in a species given the narrow parameters in which it is the optimal evolutionary strategy; even small changes in copulation cost or success rate are enough to cause it to be selected against. The specific conditions required for convenience polyandry to evolve explain why so few species have evolved convenience polyandry.

The model predicts that species which show a large coefficient of variation in male harassment traits are more likely to show the evolution of convenience polyandry because this creates large variation in costs of resisting males under each strategy. Convenience polyandry is also likely to evolve if the cost of copulation is high or there is large variation in male mating rate.

The model has posed several avenues for future research. A meta-analysis of studies exhibiting male coercion would be useful to identify correlation between coefficient of variation in male harassment trait and incidence of convenience polyandry. Other constructive studies would aim to understand the relationships between costs and female survival and harassment trait and male survival in species that exhibit convenience polyandry. Further empirical work would be valuable to accurately parameterise the female cost functions; the l’ow cost, low success response’ fee, ‘high cost, high success response’ fee and subsequent copulation fees. Very few studies exist parameterising the costs related to mating of any species because these are empirically very difficult to measure. A final study which would prove interesting would aim to investigate how and if female strategy of species with convenience polyandry evolves over time. This may involve a multigenerational experiment where the incidence of female use of each strategy is compared between the first and last generations. This would identify whether convenience polyandry is a transitory stage of evolution between singular population strategies of use a ‘high cost, high success strategy’ against all males and use a ‘low cost, low success strategy’ against all males.

## CHAPTER 5

# Using behavioural studies to improve modelling accuracy

## 5.1 Introduction

The model of convenience polyandry I presented in chapter identified factors important to the evolution of convenience polyandry. Here I present a behavioural study of *Coelopa frigida* and *Coelopa pilipes* that further investigates two of these factors; first the shape of the relationship between female costs and survival and second the actual costs of female resistance versus female copulation. The results of these studies will provide feedback on the accuracy of the model in Chapter 4. Other studies have shown the importance of establishing the female optimal mating rate but here the aim is to investigate first if one actually exists for coelopids or if the cost function follows some shape other than linear (Arnold & Meade, 2004). Measuring any costs to fitness of traits of behaviour is notoriously empirically difficult and here a method of separation of the costs of mating and resistance is tested for the first time on the coelopids.

### 5.1.1 The female cost of mating multiply

How sexual selection invokes costs is widely discussed throughout the literature. For example the cost of having sexually selected traits or the cost of raising young or the cost of polyandry (Nur, 1984; Michiels & Dhondt, 1990; Chapman et al. 1995; Chapman et al. 2003). The cost of sexually selected traits is often measured as the size of the trait covaried with the fitness it bestows on its carrier; this is the sexual selection gradient (Jones et al. 2009; Fritzsche & Arnqvist, 2013). The larger the covariance the more effect the trait has on fitness and the steeper the gradient is. This has proven useful for comparing the degree of sexual selection between males and females of the pipefish, *Syngnathus typhle*, with different sex ratios (Jones et al. 2000). *Syngnathus typhle* is a sex-role-reversed species where the males carry the young and incur the most costs of mating. Fish were kept in tanks of varying sex ratios and then genetic techniques were used to determine how offspring production varied under sex ratio. Jones *et al*. (2000) calculated the sexual selection gradient for the species and concluded multiple mating is more costly for male pipefish than females, likely due to the sex role reversal.

Here the aim is to consider a different aspect of the costs of sexual selection. Here the aim is to investigate the effect of exposure of female coelopids to multiple males and the subsequent cost multiple mating attempts and harassment bring to females. Studies in other species have considered the cost of multiple mating on females for example in the dung flies (*Sepsis* Spp.). Female dung flies risk serious injury from spiky male genitalia during copulation so mating is considered costly. Females try to minimise the number of mating encounters they receive by engaging in a pre-mating struggle with the male where she shakes violently to try and get him off her back (Ward et al. 1992). Blanckenhorn et al.'s (2002) study measured the costs multiple mating exerted on female dung flies through decreased survival, changes in egg laying and offspring production and internal injury from male genitalia. They showed that mating was extremely costly to females as it increased internal scarring which significantly increased death rate and decreased offspring production.

Formal standardised methods of measuring the costs of sexual selection such as the sexual selection gradient are limited because they assume costs are linear. There is mounting evidence the costs of sexual selection are not linear however particularly in relation to mating rate. Honkola et al. (2011) show in a live bearing fish, *Heterandria formosa*, that there is a trade-off between multiple matings guaranteeing successful fertilisations and multiple fathers of a brood causing the offspring to be smaller and take longer to develop when they were born. In another study of water striders, *Aquarius paludum*, Ronkainen et al. (2010) also showed fitness with number of matings increases for females then decreases suggesting an optimal mating rate occurs at low to intermediate numbers of matings. In a study of the effect of multiple mating on offspring production of bean weevils, *Callosobruchus maculates*, Arnqvist et al. (2005) concluded that females had two strategies to maximise their fitness; mate with many males or mate with few males. Before mating male bean weevils present females with a nuptial gift, but during mating the male's spiky genitalia scars the inside of the female. A female can either accept the scarring from mating with many males but be compensated by receiving many nuptial gifts to eat, or mate with only a few males, receive sufficient sperm to fertilise her eggs and minimise the damage to her body. A meta-analysis of 122 different insect studies by Arnqvist & Nilsson (2000) conclusively showed that the costs and benefits of multiple mating produced a non-linear relationship and it was likely that for many polyandrous species an optimal mating rate exists where the female maximises the benefits of mating and minimises the costs.

The first part of this study aims to reflect on the relationship between multiple mating and female costs in coelopids. This relationship was assumed to be linearly decreasing for the model of convenience polyandry presented in Chapter 4 and this study is to test whether that assumption is justified.

### 5.1.2 Separating the female costs of harassment and copulation

Beyond measuring the general effect of multiple matings in female fitness, measuring the cost of individual mating behaviours is complicated. Factors that may cause a female to incur costs of mating include decreased longevity, time wasted that could otherwise be spent foraging, increased risk of predation, energy loss during pre-mating struggles or energy lost due to egg laying (Arnqvist 1989; Fowler & Partridge 1989; Rice 1996; Fedorka & Mousseau, 2002; Jacob & Boivin 2004; Chapman *et al.* 2005). A female may incur benefits either directly or indirectly (Cameron et al. 2003). A direct benefit a female herself feels in her lifetime, for example if the male allows her to eat parts of his body or presents her with a food gift or provides her with some form of protection from predators or other males (Watson et al. 1998; Iyengar & Eisner, 1999; Arnqvist & Nilsson, 2000; Blackenhorn et al. 2002; Nilsson et al. 2002; Arnqvist et al. 2004; Arnqvist et al. 2005;

Sakurai & Kasuya, 2007; Hollander & Gwynne, 2009; Rankainen et al. 2010; Homkola et al. 2011). An indirect benefit will not increase her fitness but her offspring's fitness, for example her male offspring may benefit if she mated with a particularly sexually coercive male and they too grow up to be particularly sexually coercive. If her male offspring receive a fitness benefit from her mate choice, she receives an indirect fitness benefit but it is considered unlikely that an indirect benefit would ever outweigh a direct benefit (Cameron et al. 2003).

The arctiid moth (*Utetheisa ornatrix*) is a species who appear to exhibit both direct and indirect benefits of mating to females. Female arctiid moths receive direct benefits through mating with many males; male ejaculate contains protective chemicals that deter predators from eating her eggs (LaMunyon & Eisner, 1994). Female moths mate multiply to increase her direct benefits from ejaculate but a female moth is able to choose which sperm fertilise her eggs preferring the sperm of males with the largest spermatophores. LaMunyon & Eisner (1999) used a two-generation mating experiment and were able to show that large males confer an indirect benefit to females because their respective offspring had large body size spermatophores, which gave them an advantage in mating. While many studies exist that measure the cost of multiple mating few exist that measure the costs of individual mating behaviours. Two flagship studies exist however; one in water striders and the other in adzuki bean beetles (Watson et al. 1998; Sakurai & Kasuya 2007). The study of water striders has already been referenced in Chapter 4 where it was used to help parameterise the model (Watson et al. 1998). Male water striders (*Heteroptera* Spp.) harass reluctant females into mating and it is presumed that female water striders incur costs from mating due to energetic costs of fighting to escape the mating attempt, increased risk of predation during mating and decreased ability through time lost to hunt for food and it is assumed these costs of resisting must be less than the costs of mating (Arnqvist, 1989; Fairbairn, 1993; Rowe, 1994; Watson et al. 1998). The Watson et al. (1998) study used the effect of mating and resisting behaviours on respiratory rate as a measure of the instantaneous costs of increased metabolism. Using changes in carbon dioxide production as an indicator of respiratory rate an estimate of metabolism was calculated for pairs of water striders during different mate and resist behaviours and this was used to represent the energetic costs of mating. The study was able to show that during copulation females exhibit an increase in metabolism by 24%, and by 12% when they were resisting male harassment. This was the first, and remains one of the only, study to measure and separate the differences in cost of pre-mating struggles and actual copulation

The study of adzuki bean beetles, *Callosobruchus chenensis,* was an attempt to separate the costs of mating and the costs of harassment (Sakurai & Kasuya 2007). Like water striders, adzuki bean beetles are an insect species with a polyandrous mating system of harassive males and resistive females. Sakurai & Kasuya (2007) compared the effects of mating females to either normal males or ablated males after an initial exposure of the female to a normal male to ensure oviposition. Normal males were allowed to mate with a female undisturbed; females received harassment and mating. Males in the ablated group were anaesthetised as soon as they began to copulate and the male's oedagus was cut to sterilise him before revival to continue copulating and harassing the female. Females mated with ablated males received costs of harassment but no costs of mating because their mates were sterile. The study showed ablated pairs produced 18.6% fewer offspring than normal males but failed to measure any significant costs to the females due to mating.

The second part of this study aims to separate and quantify the costs of mating interactions of coelopids. The coelopids exhibit convenience polyandry and the model in Chapter 4 parameterises the high cost, high success fee, $\theta_F$, the low cost, low success fee, $\theta_A$, and the copulation fee $\mu$. Here this chapter aims to separate the costs of either resistance response, high cost or low cost, from the copulation fee.

## 5.2 Methods: Behavioural Studies

### 5.2.1 Animal husbandry

#### *Breeding from a wild population*

Initial wild populations of coelopids were collected from East Wemyss in Fife, Scotland as larvae and stored at 25°C to promote development. The preferred species for these studies is *Coelopa frigida* however after the first trials *C. frigida* became unexpectedly rare to find in the wild so *Coelopa pilipes*, a closely related species, were collected when no *C. frigida* could be found. Both species exhibit similar mating systems involving energetic pre-mating struggles however only *C. frigida* appears to exhibit convenience polyandry. Individuals of *C. pilipes* have darker coloured bodies than *C. frigida* and males of *C. pilipes* are characterised by the dense hairs on their legs (Edward & Gilburn, 2007). Individuals show large variation in longevity and are expected to live between 2 and 14 days (Butlin & Day, 1985).

Two species of brown algae, *Laminaria digitata* and *Fucus serratus*, were collected from the same location as flies and stored in deep freeze. Seaweed stimulates sexual activity in both species of fly; *C. frigida* is most stimulated by *L. digitata* and *C. pilipes* is most stimulated by *F. serratus* (Edward & Gilburn, 1007). Seaweed provides a site for egg laying (oviposition) where larvae feed on microorganisms growing in the decaying seaweed (Cullen *et al*, 1987; Edward *et al*, 2008).

Adults were collected from the wild populations and 30 (15 male and 15 female) were transferred to a breeding cage. This consisted of a clear-sided plastic box 12" square with a blue pop-on lid. In the bottom of the container was placed a quarter inch layer of defrosted and minced seaweed, to act as a sexual stimulant and to provide an oviposition site for egg laying (Dunn et al. 1999). A large (6"x4") hole was cut Into the lid of the Tupperware box and covered with blue-roll to allow airflow. The cage was inspected daily and if the population appeared to be becoming very dense it was split into two and half the population was moved to another similarly prepared breeding cage and adding extra minced seaweed to both cages. Appropriate seaweed use is *Laminaria digitata* for *C. frigida* and *Fucus serratus* for *C. pilipes* (Dunn et al. 1999).

The breeding cage and kept in the warm box at 25°C, 12 hour on/off daylight patterns and 60% humidity. As soon as the first virgin flies began to emerge they were harvested. To harvest the flies the breeding cage was opened in a darkened room next to a fluorescent strip light. Coelopids are phototactic so using the light makes them easier to catch. Coelopids become sexually mature after approximately 18 hours so to prevent early emerging flies mating all flies were removed from the cages twice daily (Dunn et al. 1999).

### *Sexing flies*

When virgin flies were harvested they were quickly separated by sex to be stored in the refrigerator. To sex the flies they were gently anaesthetised using carbon dioxide. Flies were sexed by visual inspection on a $CO_2$ inspection stage; male *C. frigida* have a round tan coloured abdomen with a black dot marking their aedeagus and females have a dark, shiny, pointed abdomen. Male *C. pilipes* are large, dark coloured and have extremely hairy legs.

### *Storing virgin flies*

Flies were stored in plastic conical flasks with foam stoppers to allow for airflow, males and females were stored separately. Cotton wool soaked in sucrose solution was used as a food source and refreshed every 3 days. Flies were not used after they had been in the fridge for longer than 15 days.

### *Preparation for usage*

Before use, male flies were removed from the fridge and individually stored in a conical flask with 15g of seaweed, *Laminaria digitata* for *C. frigida* and *Fucus serratus* for *C. pilipes*, to provide stimulation of sexual behaviours and a ball of cotton wool soaked in sucrose as a food source (Phillips et al. 1995). Female flies were stored in groups in bottles with sugar solution. All flies were moved to the warm box for 24 hours prior to commencement of study to warm them up and ensure full sexual maturation.

### 5.2.2 Experimental Design: The cost of multiple mating in Coelopids

Virgin female *Coelopa pilipes* were stored in individual conical flasks along with 15g of minced *Fucus serratus* seaweed as a sexual stimulant and oviposition site and a ball of cotton wool dipped in sucrose solution as a food source. Each female was paired with 1, 5 or 10 males. Cages were returned to the warm box and kept on 12 hour light/dark cycles. Every 12 hours the cages were inspected and the number of males and females alive in each was recorded. After all flies had died naturally the cages were inspected for egg clutches and any eggs were counted. This was repeated using *C. frigida*. Initially 49 females of *C. pilipes* were used; 16 paired to a single male, 16 paired to 5 males and 17 paired to 10 males. Of *C. Frigida,* 32 females were initially used; 9 paired to a single male, 11 paired to 5 males and 12 paired to 10 males. Cages were disregarded if the female or all the males had died within the first 24 hours for unknown reasons or if the females escaped; of the initial females 26 *C. pilipes* and 25 *C. frigida* provided usable data.

An individual was assumed to be alive up to the moment they were found dead. Male average survival was calculated by multiplying the size of each time interval by the number of males alive at that moment and creating a cumulative time total which after the final male's death was divided by the original number of males to give the mean. Species were analysed separately then their results were pooled and they were analysed together. Two sample t-tests were used to analyse the differences in female survival and average male survival with number of males for groups 1 male and 5 males, 1 male and 10 males and 5 males and 10 males. It was also tested for correlations between female life span and average male life span against number of males.

### 5.2.3 Experimental Design: Separating the costs of female mating and resisting in Coelopids

Half the virgin males were individually anaesthetised with $CO_2$ and laid on their backs on the ceramic inspection plate. A thin needle was used to gently move their wings away from their body while another needle was heated in a Bunsen burner and carefully applied to their oedagus to cauterise the males as a sterilisation procedure. Cauterised males were then returned to the warm box for 24 hours to recover. Cauterised males were carefully inspected for injury. All males recovered fully but in comparison to their non-cauterised counterparts appeared to move slightly slower.

All virgin females were initially paired with one normal male and observed to confirm one mating occurred then separated. This was to ensure every female had at least one mating for both groups (Sakurai & Kasuya, 2007).

Females were then paired with either cauterised males or normal males. Each pair was observed for the first five minutes to ensure interactions occurred. After the first 5 pairings it became apparent the cauterised males were not interacting at all with females. After observation time was increased to 15 minutes for the rest of the cauterised males no interaction between cauterised males and females were recorded. All males were left with their paired females until death and presence or absence of eggs and offspring was recorded.

## 5.3 Results

### 5.3.1 The cost of multiple mating in coelopids

No significant difference in female survival for *C. pilipes* was shown between groups of females that were exposed to 1, 5 or 10 males. There was a significant effect on male survival however; those males who had been in groups of 10 had significantly shorter lives than single males (Table 5.1a).

There was a significant difference in female survival between all groups for *C. frigida* and there was a negative correlation between female survival and the number of males they were exposed to (figure 5.1; $r = -0.629, p = 0.001$). There was no significant difference in male survival between any of the groups (Table 5.1b).

*Coelopa pilipes* males lived significantly shorter lives than *C. frigida* across the board ($p = 0.000$). However the only significant difference between groups was for 10 males (Table 5.2); *C. pilipes* lived shorter lives than *C. frigida* when they were in groups of 10 ($p = 0.001$).

Frustratingly, neither *C. frigida* nor *C. pilipes* laid any eggs for entirely unknown reasons on any of the occasions this experiment was run; no egg counts were recorded.

### 5.3.2 Separating the costs of female mating and resisting in Coelopids

No cauterized male was observed interacting with a female; they ignored them completely. While eggs were found in all cages, some were even hatched, they were disregarded because the first male pairing would bias them since no interactions with cauterised males had occurred to increase harassment costs. Females that were mated with normal males all produced eggs and all cages showed some hatched eggs.

**Table 5.1: Comparison between mean longevities of species.**
Mean female survival of one group compared to mean female survival of another. Mean male survival of one group compared to mean male survival of another. Null hypothesis states group mean survival lengths are not equal.

A. **Comparison of *C. pilipes* groups.** Males in groups of 10 lived significantly shorter lives than single males.
B. **B. Comparison of *C. frigida* groups.** Female survival is significantly different between all groups.

| | | | Two sample t-test | | | |
|---|---|---|---|---|---|---|
| | | | Differences in mean female survival | | Differences in mean male survival | |
| | Species | Group Comparison (f:m vs f:m) | Degrees of freedom | P-Value | Degrees of freedom | P-Value |
| **A.** | *C. pilipes* | 1:1 vs. 1:5 | 15 | 0.505 | 15 | 0.324 |
| | *C. pilipes* | 1:1 vs. 1:10 | 13 | 0.765 | 12 | 0.068* |
| | *C. pilipes* | 1:5 vs. 1:10 | 11 | 0.813 | 13 | 0.371 |
| **B.** | *C. frigida* | 1:1 vs. 1:5 | 12 | 0.089 | 10 | 0.246 |
| | *C. frigida* | 1:1 vs. 1:10 | 13 | 0.003* | 9 | 0.396 |
| | *C. frigida* | 1:5 vs. 1:10 | 15 | 0.049* | 15 | 0.594 |

* Significant at the 95% confidence level

**Table 5.2: Comparison of mean longevities between species. Mean female survival of one group compared to mean female survival of another.**
Mean male survival of one group compared to mean male survival of another. Null hypothesis states group mean survival lengths are not equal.

A. **Comparison of mean female survival.** Males in groups of 10 lived significantly shorter lives than single males.

B. **Comparison of mean male survival.** Female survival is significantly different between all groups.

**Female survival**

| | | *C. pilipes* | | *C. frigida* | | Difference between means (2 sample t-test) | |
|---|---|---|---|---|---|---|---|
| **A.** | Group ratio (female:males) | Mean | St Dev | Mean | St Dev | Degrees of Freedom | P-value |
| | 1:1 | 65.1 | 12.7 | 78.6 | 13.4 | 12 | 0.063 |
| | 1:5 | 61.44 | 9.91 | 66.2 | 13.0 | 14 | 0.396 |
| | 1:10 | 63.0 | 15.5 | 51.6 | 15.9 | 14 | 0.156 |

**Male mean survival**

| | | *C. pilipes* | | *C. frigida* | | Difference between means (2 sample t-test) | |
|---|---|---|---|---|---|---|---|
| **B.** | Group ratio (female:males) | Mean | St Dev | Mean | St Dev | Degrees of Freedom | P-value |
| | 1:1 | 54.0 | 13.6 | 78.6 | 13.4 | 11 | 0.095 |
| | 1:5 | 47.9 | 11.8 | 66.2 | 13.0 | 15 | 0.073 |
| | 1:10 | 43.44 | 7.62 | 61.9 | 10.4 | 14 | 0.001* |

* Significant at the 95% confidence level

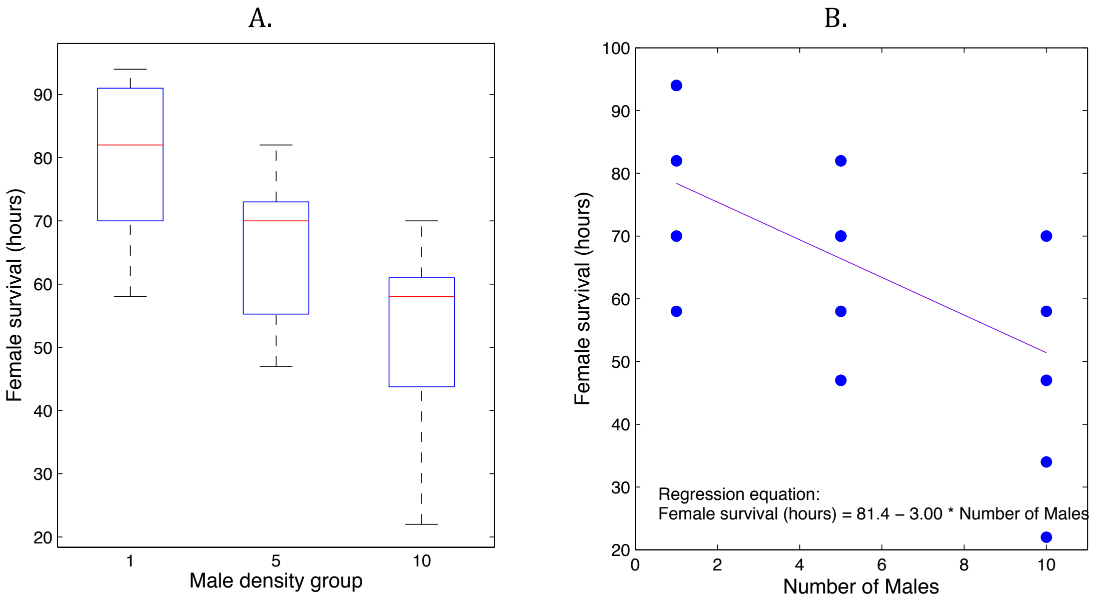

**Figure 5.1. Female survival in C. Frigida is negatively correlated to the number of males they mate with.**

A. **Box plot of female survival against number of males they were exposed to.** Significant differences were found between the mean survival of each group
B. **Scatter graph and plotted regression line of female survival and male exposure.** Unfortunately due to the limited number of successful trials it is not possible to draw accurate conclusions about the shape of the relationship between female mating rate and survival in *C. frigida*. However the data does show at least that the relationship is likely to be negative.

## 5.4 Discussion of the behavioural studies

In this study first female *C. frigida* were paired with cauterised or non-cauterised males and observed to separate the costs of harassment and mating. Secondly female *C. frigida* and *C. pilipes* were exposed to different numbers of males to examine the effect of multiple males on female survival and fecundity. This work should be considered a pilot study; it indicates the experimental design may reveal interesting details but is insufficient as a standalone study to draw strong conclusions.

### 5.4.1 *C. frigida* shows a negative relationship between mate number and female survival

The first result of this study is female survival of *C. frigida* is negatively correlated to the number of males they were exposed to. There was significant difference in survival between females exposed to one male and females exposed to ten males. Unfortunately, due to the low number of successful trials it is not possible to draw conclusions about the shape of the relationship between mating rate and female survival.

The experimental design could be improved. It could be argued that in the wild *C. frigida* is expected to be 'extremely promiscuous' (Blyth & Gilburn, 2006) so the choice of number of males used may be unrepresentative of the wild and even with 10 males the costs may still be low. Perhaps increasing the range of male groups to up to 100 or 150 males, or even more, to a single female would be useful. If a wider range of group sizes were used this would increase the resolution of the function that could be estimated to best fit the data too. It would be interesting to know the effect of large numbers of males because fitness cannot linearly increase indefinitely. Unfortunately it is difficult to breed such high numbers of males because of the rapid sexual maturation of the species, their relatively short life span and apparently decreasing abundance in the wild (A. Gilburn, personal communication). Breeding such high numbers of males that would be required to do multiple repeats of each group size is difficult without doing multi-generational breeding from within laboratory populations which increases the risk of inbreeding depressions, the effects of which are currently unknown in coelopids. Handling the number of insects that would be required to find so many males would also rapidly become unmanageable for a loan worker. Noteworthy is that although the maximum number of males the female was exposed to was only 10, they were kept crowded together in a small container so the population density is potentially higher than they might experience in the wild. This is likely to magnify any costs that did occur.

It is unfortunate that none of the females laid eggs. Egg-laying is hypothesized to be a main source of cost of reproduction in some species, estimated as up to 57% of the costs of oviposition in some examples, and for the female coelopids to not lay eggs suggests that they may not have incurred the full costs of mating (Rosenheim, 1999; Yanagi & Miyatake, 2003; Rosenheim et al. 2008). It should however be noted that in a previous study of *C. frigida* the exposure of seaweed, which triggers oviposition, was found to decrease female survival slightly but the mere presence of males further reduced survival by 40% (Meader & Gilburn, 2008).

It is difficult to decide whether this study underestimated the costs of mating because of the conflict of low numbers of males versus high density of males and the confusion of the extent of the role of oviposition in coelopids costs. Further repeats of the study would be useful as confirmation of the results and future studies would benefit from increased number of male exposures and getting the females to successfully lay eggs. Further enhancements that could be made would involve observing the females for the duration of the matings and recording the frequency and duration of interactions with males. This study does not distinguish between female life costs due to increased mating rate or female life costs due to any other factors that comes as a by-product of increased exposure to multiple males. Observation of the female would provide insight into where her time was spent and perhaps a better understanding of which parts of the mating interaction were most costly.

### 5.4.2 The costs of mating may be higher in C. frigida than C. pilipes

The second result the multiple mating study showed is the difference in effect of multiple mates between the two species of coelopid. The species *C. frigida* showed a significant decrease in female survival as the number of males a female was matched with increased. No effect was recorded in *C. pilipes.* This indicates either the cost of mating or the level of harassment is higher in *C. frigida* than *C. pilipes.*

The third result the study showed was male average survival decreased as group size increased. This could suggest that increased density of male increases their willingness to mate and causes them to use more energy on reproduction rather than survival or that male-male competition is costly and decreases male survival. The latter seems most likely because it would be expected that an increased willingness to mate be reflected in a decrease in female survival if females were being harassed more. Understanding how male costs work would allow for better understanding and modelling of male fitness. This could be used to improve the male fitness equation in Chapter 4. Previous studies have suggested there may be search costs to the male finding a mate (Gotthard et al. 1999; Meader & Gilburn, 2008). While search costs in this study are highly unlikely due to the small mating cages, perhaps males will incur significant costs from male-male competition or failed mating attempts or even homosexual mating attempts as has been observed in many other species of insects (Aiken, 1981; Harari et al. 2000; Serrano et al. 2000; Edvardsson & Tregenza, 2005 Burgevin et al. 2013). It will require careful observational experiments to identify the main source of costs to male coelopids.

### 5.4.3 Male Cauterisation is not an effective method of sterilisation of Coelopids

The main result of the individual mating study was negative; cauterisation of male coelopids to separate the female costs of mating and harassment is an ineffective method. However this study has shown that male cauterisation is an effective method of sterilisation and that sterilised males appear to lose their willingness to mate.

Cauterising males' oedagi with a flamed needle was not found to be an effective method of separating the costs of mating and harassment because it resulted in male flies who would neither mate nor harass females so imparted neither a mating cost or a harassment cost on the female. Cauterised flies were never observed mating and when left for several days with a virgin female no eggs hatched. In their 2007 experiment on the adzuki bean beetle, Sakurai & Kasuya paired females with normal males and upon copulation anaesthetised and ablated some males while they were still attached to the female. This would be useful if it could be used on *C. frigida* as it would allow males to still harass females then be stopped from mating however it would be much harder to carry out this procedure on *C. frigida* without damaging male or female and incurring further costs. It would also prevent the male from repeating harassment attempts which would bias the costs. Later in their study, Sakurai & Kasuya (2007) used a radioactive cobalt source to sterilise male adzuki beetles so they could do further tests about the effect of multiple males on the female. They had evidence that beetles sterilised in this manner will mate with and fertilise females but none of the eggs will hatch (Hussain & Imura, 1989). Sakurai & Kasuya (2007) chose to use ablated males with their oedagi removed over irradiated males in their cost of harassment study but it would have been interesting to see if using males sterilised in this manner produced different numbers of fertilised eggs than ablated or normal males did. This would be an interesting technique to experiment on coelopids with. If the effects of radiation on coelopids sterilised them but did not reduce their sexual interest, this would be a useful alternative method to ablation by cauterisation, that could allow future studies to more successfully separate the costs of mating and harassment in the coelopids.

In a seminal study of *Drosophila melanogaster* individuals were genetically engineered to be incapable of laying eggs, yet still mated with males. This effectively allowed for the separation of the costs of egg laying from the other costs of reproduction (Chapman et al. 1995; Yanagi & Miyatake, 2003). This would be difficult and expensive to do with

Coelopid. Another interesting method however of separating the costs of mating from the costs of harassment would be to prevent mated females from finding an oviposition site and laying eggs and then measuring the differences in longevity (Yanagi & Miyatake, 2003). It is unclear as to how effective this would be with coelopids because of the un-quantified roles of seaweed as a trigger of oviposition versus presence of male as cost inducing mechanisms, but would be worthy of future exploration (Meader & Gilburn, 2008).

### 5.4.4 Encouraging Coelopids to oviposit was difficult

Despite previous studies showing virgin and non-virgin females will both lay equal numbers of eggs in the presence of seaweed it was frequently a struggle to get females to lay eggs (Dunn et al. 2002). To investigate a further study was conducted into the effect of the type of seaweed used, *Laminaria* is commonly used as the preferred seaweed for *C. frigida*, however the effect of using *Ascophyllum* seaweed was compared with *Laminaria* (methods and results detailed in appendix 11). Perplexingly eggs were laid on both seaweeds with *Ascophyllum* being favoured. Although this now questions the use of *Laminaria* for *C. Frigida,* thus far it does suggest that type of seaweed was not the reason no eggs were laid in most of the previous stages, as eggs were laid in the *Ascophyllum* and *Laminaria* studies.

Other factors that could possibly influence the females egg laying are quantity of seaweed provided for oviposition, temperature, humidity, age at breeding and excessive exposure to $CO_2$ anaesthetic but all these factors were controlled and kept constant as far as possible and still resulted in mixed results in egg laying. Desiccation in the warm box proved to be a problem in early trials and increasing humidity of the warm box only caused a tall, white, spindly fungus to grow which could cover an entire breeding cage in less than 12 hours. Increasing the amount of seaweed used was found as an alternative and more effective method of avoiding desiccation. In early trials excessive exposure to anaesthetic due to poor animal handling skills was another problem and resulted in insects that demonstrated sluggish behaviour even once the anaesthetic had worn off. Using a mouth pooter rather than $CO_2$ solved this problem whenever it was necessary to move animals and also designing experiments such that minimal movements of animals between cages was necessary. Other factors that could have influenced egg laying were difference in wild populations, populations were bred from wild collections taken on three different occasions, and the *Laminaria* stock being used being polluted somehow. The latter reason is perhaps the most likely as egg laying problems only occurred in the second half of experiments and the seaweed stock was replenished only once during the trials. Of note future studies should ensure that seaweed is stored frozen and remains frozen for as long as possible before use; decaying seaweed over 2 days old appears to begin to lose its effect on the flies.

## 5.5 Validating the convenience polyandry model

### 5.5.1 Female costs and survival

The results of the multiple mating study provides data that lends support to the assumptions of the effect of female costs on female survival. The results of the multiple mating experiment were insufficient to show a linear relationship is the best estimate of female survival against exposure to males, more data points are required to confirm linearity (figure 5.1). The data shows the relationship between female mating rate and survival is decreasing in *C. frigida*, but the data was insufficient to make conclusions about the shape of the functional relationship.

The convenience polyandry model has a female fitness equation of the form:

$$W_F = R_F \times S_F$$

(Eqn 5.1)

Where

$$S_F = 1 - \phi C_F$$

(Eqn 5.2)

Where $R_F$ is reproductive benefits due to mating and $S_F$ her survival depreciation due to the costs of mating, $C_F$. This form of fitness equation assumes the relationship between survival and mating cost is negative and linear. This study provides evidence to support that the relationship is negative but more data is required to draw conclusions about the shape.

### 5.5.2 The costs of resistance and copulation

The second part of the study aimed to provide species-specific estimates of the costs of resistance strategies and the cost of copulation. In the model these were the female fight behaviour cost, $\theta_F$, the female acceptance behaviour cost , $\theta_A$, and the cost of copulation , $\eta$. The experimental design, had it been successful, would have provided an overall estimate of the cost of any resistance strategy which would have been useful to show the model was at least using an appropriate estimate. Ideally each interaction between female and cauterised male or normal would also have been observed and then time spent using each resistance response could have been recorded and the costs of each strategy separated. In the future if a method for sterilising males yet still encouraging them to attempt a mating is identified this would be useful to also do.

## 5.6 Conclusions

This study has indicated there is a decrease in female fitness with increasing mating rate; not an optimal mating rate. Presumably this is countered in the wild because female mating rate is so extremely high (Blyth & Gilburn, 2006). It would be useful to repeat the study with a higher resolution of exposed male groups and be able to have the females successfully lay eggs and count them. It would also be useful for future studies to investigate the costs on males to shape the male fitness equation more accurately. This study should be considered a pilot study as it indicates the experimental design will reveal further insight on the relationship between female mating rate and cost in coelopids.

From this study it can definitely be concluded male cauterization is an inappropriate method to distinguish the costs of mating from the costs of harassment in *C. frigida*. It can also be concluded that cauterized male coelopids are not interested in sex. This study is a good example of the difficulties faced in testing and validating models and shows how it is useful for mathematicians to understand the empirical methods.

## CHAPTER 6

# Discussion

This thesis presented studies of two systems where the evolution of sexual behaviours have evolved through trade-offs between male and female costs. The purpose of this thesis was to reflect on the roles of natural and sexual selection as opposing or complementary forces of selection in each study system and advance theoretical understanding of the evolutionary mechanisms in both studies. The first study, of avian protandry, investigated the role of sexual selection in the adaptation of species to changing environment. The second study, of convenience polyandry, has advanced our understanding of the role of sexual selection in the evolution of convenience polyandry. This has paved the way for future work to consider the advantages sexually antagonistic coevolution may give species in adaptation to changing environments.

This chapter revisits the aims of the thesis. First this chapter summarises the key results from both study systems and all chapters. It details how the thesis has furthered theoretical understanding of the evolution of protandry in avian migration and convenience polyandry in species exhibiting male harassment and female resistance, fulfilling Aim 1. This chapter then reflects on what the work of the thesis has revealed about the role of natural and sexual selection as opposing or complementary forces in both study systems, fulfilling Aim 2. This chapter considers what can be gleaned from the thesis on the role of sexual selection in providing advantages in the adaptation of species in response to changing environment in the protandrous migratory avian species. It also considers what is necessary to understand if species that exhibit convenience polyandry have an advantage in adaptation to changing environment. Finally this chapter reflects on possible avenues for future work.

## 6.1 Aim 1: Furthering theoretical understanding of avian protandry and insect convenience polyandry

### 6.1.1 Chapter 2

Chapter 2 presented a series of models that tested each of the main proposed hypotheses for the early arrival of male birds to spring breeding ground, namely the rank advantage, the mate opportunity and the susceptibility hypotheses (Morbey & Ydenberg, 2001). The work was novel because there existed only two models of protandrous avian migration prior to this and this work presented the first models to test each hypothesis in combination with the others and present an integrated framework considering all the hypotheses simultaneously. The methods were novel because they allowed the models to consider the evolution of the population through its width of distribution as well as mean arrival dates; this provided an encompassing view of the effects of individuals on the entire population.

The results of the work contribute to the theoretical understanding of protandrous behaviour in avian species because they further iron out some of the limitations of the theoretical hypotheses. The main results of Chapter 2 illustrated the importance of environmental factors and sex biased responses to environment on the evolution of protandry. The results also showed that the rank advantage and mate opportunity hypotheses alone are insufficient to explain the evolution of protandry but combined with the susceptibility hypothesis or each other could provide a mechanism for evolution. The models also highlighted the importance of understanding the arrival patterns of the whole population not just the first arrival or mean arrival dates. This provides an immediate utility for the results because it alerts empiricists to the importance of careful observation of arrival of the entire population for future studies of protandry.

### 6.1.2 Chapter 3

Chapter 3 further explored the results of Chapter 2. Chapter 3 investigated the importance of environmental effects on the evolution of protandry. Global mean temperatures are increasing and there is increasing uncertainty in between-year environmental conditions and avian species already show advancement of arrival dates of both sexes in the face of climate change. (Crick et al. 1997; Ivanauskas et al. 1997; Bradley et al. 1999; Crick & Sparks 1999; Giorgio & Francisco, 2000; Butler 2003; Root et al. 2003; Hüppop & Hüppop 2004; Lehikoinen et al 2004; Marra et al. 2005; Rainio et al. 2007; Ruboilinio et al. 2007; Thorup et al. 2007). Chapter 3 aimed to understand what may happen to protandrous bird species faced with climate change when protandry is driven by the rank advantage, mate opportunity or susceptibility hypotheses. The work in Chapter 3 is novel because it presents the first modelling study to consider the role of each sex in the evolution of protandry under climate change.

The results of Chapter 3 furthered theoretical understanding of avian protandry by showing that climate change should generally advance arrival dates of protandrous species and species that were most likely to show the largest adaptations to climate change through protandry are those which are affected by all three hypotheses. The results also showed species who receive a rank advantage of early arrival are unlikely to show changes in degree of protandry under climate change. However non-protandrous species who may receive an advantage of early arrival could evolve protandry to a small degree to maximise their fitness under climate change.

This work is important because it draws attention for the need to empirically investigate the effect of climate change on protandrous avian species. Climate change is causing some species to change their migratory stop overs and resulting in new areas being used as breeding grounds for many thousands more birds than would normally be expected (Spottiswoode & Saino, 2010). This can have detrimental effects on agriculture. An example of this occurs in Norway where government subsidies have been introduced to compensate farmers for crop damage caused by escalating numbers of migratory geese arriving (Eichorn et al. 2009; Tombre et al. 2013; Madsen et al. 2014). This is an example of a cascade effect climate change can cause. To anticipate further damaging effects that may arise from conflict with birds adapting to climate change it makes sense to understand all elements of avian migration as fully as possible.

### 6.1.3 Chapter 4

Chapter 4 presented a model of convenience polyandry and used the coelopids as an example to parameterise it. In such species, males harass females for mating and both harassment and copulation are costly. Females may respond to males with a high cost, high success response strategy or a low cost, low success response strategy. Females use a high cost response to resist coercion from most males unless she deems the costs of trying to resist a particular male outweigh the costs of being coerced into copulation with him in which case she may choose to 'give in' and use a low cost, low success response. This is convenience polyandry and theory dictates this evolves as a strategy for the female to minimise her costs of mating (Thornhill & Alcock, 1983). The work in chapter 4 is novel because it is the first study of convenience polyandry modelling the costs and benefits to the female and allowing sexually antagonistic coevolution between female strategy and male size.

The results of Chapter 4 furthered theoretical knowledge of the evolution of convenience polyandry by identifying the narrow window of conditions necessary for it to evolve and this likely explains why the number of species that exhibit convenience polyandry is low. The model predicts that species which show a high coefficient of variation in male harassment trait are most likely to evolve protandry. This is because variation in male trait causes variation in costs and success of each response strategy to the females and a mix of responses is her optimal strategy. Chapter 4 identified the importance of empirical studies that could estimate the relative costs of mating behaviours and copulations.

The work in Chapter 4 is important because convenience polyandry occurs throughout a wide range of unrelated species including insects, sharks, amphibians, crustaceans, birds and reptiles (Rowe 1991; Crean *et al.* 1999; Cordero-Rivera & Andres 2002; Lee & Hays 2004; Thiel & Correa 2004; Blyth & Gilburn, 2006; Sztatecsny *et al.* 2006; Trontii *et al.* 2006; DiBattista *et al.* 2008; Portroy *et al.* 2008; Adler, 2009; Johnson & Brockman 2010; Griffiths *et al.* 2011). Understanding what causes convenience polyandry in these different species could provide understanding of evolutionary mechanisms that are generalizable to a wide range of species. Convenience polyandry is an example of a behaviour evolving as males and females interact to balance their costs and benefits driven by the interaction of natural and sexual selection, understanding what drives behaviours like this could provide further insight into the role of sexual selection and thus if sexual selection can provide any advantage to species in adaptation to environmental change.

### 6.1.4 Chapter 5

Chapter 5 detailed empirical studies that aimed to identify the shape of the relationship between female costs and survival as well as separate the costs of mating and resisting in a species that exhibits convenience polyandry. The results of Chapter 5 showed female longevity decreases linearly as number of males they are exposed to increases in *C. frigida* and that the costs of multiple mating are higher in *C. frigida* than in *C. pilipes*. The study also found that male cauterisation was an ineffective method for separating the costs of mating and harassment in the seaweed flies because it renders the males uninterested in interacting with females.

This work is interesting because the shape of the relationship between female costs and fitness effects is disputed (Arnqvist & Nilsson, 2000; Kokko et al, 2012). It is also interesting because between it and Chapter 4 it provides an example of a model being built, being tested and producing a research question and the subsequent completion of an empirical study that addresses the research question.

The results of Chapter 5 lend support to the assumption of a linearly decreasing relationship between female cost and survival in coelopids used in the model of convenience polyandry in Chapter 4, but further studies are required to positively identify the shape of the relationship. The failure of the experiment to separate the costs of mating and harassment are a reminder of the inherent difficulty of estimating costs. The cost separation experiment was useful because it rules out cauterisation as a method for separating the costs of mating and resistance in the coelopids. Chapter 5 suggests alternative methods that future studies could use to separate the costs of mating and resistance in the coelopids. Chapter 5 also lists a number of suggestions for the animal husbandry of future studies and suggests methods that may encourage females to oviposit so effects on survival are more reflective of actual costs of mating.

## 6.2 Aim 2: Investigating the interaction of natural and sexual selection as opposing or complementary forces in the evolution of sexual behaviours

Comparing both study systems it can be seen that different balances of natural and sexual selection occur in different systems and the importance of each varies between systems.

In the study of protandrous migratory birds, Chapters 2 and 3 indicate both male and female costs and benefits work together sometimes and against each other at other times to define optimal arrival dates. The study of avian protandry showed that if the benefits for early male arrival appear to be high arrival could still be delayed if the costs to the females are too high. For example the delay of male arrival under the mate opportunity hypothesis with male biased survival under climate change in Chapter 3 (Table 3.4); male benefits of early arrival are high but female costs delay female arrival and consequentially male arrival. This provides an example of natural and sexual selection working as complementary forces that allows both sexes to optimise their fitness. However the protandry study also showed male and female costs may work against each other under opposing forces of natural and sexual selection. For example the integrated model with female biased survival in Chapter 2 shows that although male survival is low for males early in the season they will still arrive early, some even arriving earlier than the females, to benefit their sexually selected fitness at the cost of their naturally selected fitness (Figure 2.12c).

The study of convenience polyandry showed that the female’s balance of costs and benefits was of greater importance in determining the evolution of protandry than the male’s. Male size could stay the same over a range of parameter values whereas female strategy changed markedly. Male costs and benefits cause their size to evolve in order to maximise their mating rate but females appear to be more in control of how many matings could be achieved in total and thus in control of the population fitness. Female cost balance of strategies and copulation was important to the evolution of convenience polyandry but appeared to have no effect on male size.

that sexual selection may provide an increased ability for species to evolve their arrival date in the face of climate change however this is only the case when species can benefit from EPCs, not when there are territory benefits.

### 6.3.2 Paving the way for understanding the effect of sexual selection on adaptation of species that exhibit convenience polyandry to changing environment

The model in Chapter 4 is designed to understand the role of natural and sexual selection in the evolution of convenience polyandry; this paves the way for future studies to understand whether sexually antagonistic coevolution, or species where females show an ability to adapt their response to harassive males, may have some kind of advantage in adapting to changing environment.

The results of Chapter 4 showed convenience polyandry evolves as a result of very specific conditions and it is very easy for these conditions to be changed such that a different behavioural response strategy should evolve. Chapter 4 also showed that females are likely to evolve convenience polyandry in the face of large variation in male harassment trait. These results show that species which exhibit convenience polyandry may be able to evolve new behavioural strategies in response to small changes and conditions and often evolve in response to variation in conditions. Perhaps this indicates that sexual selection will indeed provide these species with an advantage in adaptation to changing environments as they already have responsive mechanisms in place for rapid evolution.

These examples illustrate the complexities of the role of natural and sexual selection; they are not opposing or complementary forces, they are opposing and complementary forces and which role they take is context dependent.

## 6.3 Aim 3: Exploring the role of sexual selection in aiding adaptation to changing environments

### 6.3.1 Sexual selection may aid adaptation of protandrous species in response to changing environment

From the results of Chapters 2 and 3 it can be concluded that the differential effects of natural and sexual selection on the evolution of protandry are likely to cause protandrous species to adapt to a changing environment. Of note the results of chapter 3 showed that species showing the largest incidence of sexual selection, those affected by the rank advantage, mate opportunity and susceptibility hypotheses, showed the biggest changes in response to climate change. The rank advantage model on its own never showed the evolution of protandry with or without climate change. The mate opportunity model on its own showed protandry would evolve in some simulations when climate change was introduced. The environment model on its own, which had no sexual selection, did not show protandry to evolve at any point. Considering all these results together indicates

## 6.3 Future work

### 6.3.1 Protandrous arrival of migratory avian species

In Chapter 2 the population shape was restricted to follow a normal distribution but the results of the model suggested that if the populations had been able to show positive or negative skew in the distribution of arrival dates then it would have provided further insight still into the evolution of protandry. For future work it would be interesting to design a mathematical formulation where the shape of the distribution of the population could evolve over time. The use of individual based simulations could have a potential role to achieve this.

Chapter 3 showed different results from each model in response to climate change. This calls for more long-term studies of protandrous species to be analysed for effects of climate change over the last 100 years, this would provide data that could be used to verify the model or at least show if species affected by each hypothesis show effects that mirror the results the model shows. It would also be useful for existing observational stations to become aware of the need to understand the arrival distributions of protandrous species, not just the first arriving individuals or the mean arrival date. This would allow the accuracy of future observations to be increased.

### 6.3.1 Convenience polyandry in insects and other species

Chapter 4 showed convenience polyandry occurs over a narrow range of parameters. It shows convenience polyandry is likely to evolve when the costs of copulation are within a narrow limit; too low and a singular strategy of accept evolves, too high and a singular strategy of fight evolves. Chapter 4 also showed that the balance between the costs of each strategy is important and convenience polyandry is likely to evolve when these are close. It would be interesting for future work to separate out and estimate these costs and how they compare to each other in coelopids and other species that exhibit convenience polyandry. This is what was attempted unsuccessfully in Chapter 5. Future studies could potentially achieve it using different methods for example radioactive sterilisation, cauterisation during copulation or oviposit restriction techniques (Yanagi & Mayitake, 2003; Sakurai & Kasuya, 2007).

This thesis has detailed why it is important to understand how evolutionary behaviours evolve in order to predict how they will fare in the face of environmental change. Chapters 4 provides the first modelling work understanding what causes convenience polyandry to evolve. Future work could build on this by investigating if sexual selection and sexually antagonistic coevolution can provide a benefit in adaptation to changing environment.

## 6.4 Conclusion

This thesis has shown interesting and useful results from both the protandry models and the convenience polyandry models. This thesis has contributed to the theoretical understanding of both the evolution of protandry in avian species and the evolution of convenience polyandry. This thesis has also discussed the opposing and complementary roles of natural selection in the evolution of each system and reflected on the potential for sexual selection to provide an advantage in adaptation to changing environment in each system.

In conclusion the role of natural and sexual selection in the evolution of sexual behaviours is complex and the mechanisms of evolution are intricate. Mathematical modelling is an underutilised tool in this field that brings the advantage of ironing out unintuitive details and posing relevant, empirically testable questions. The work here has indicated sexual selection in protandrous migratory avian species may provide an advantage in adaptation to changing environment to these species. The work here has also paved the way for future studies to consider the role of sexual selection in adaptation to changing environment in species where sexual conflict and pre-mating struggles occur.

As our modern environment becomes more changeable understanding the mechanisms becomes more important so species least able to adapt to future changes can be identified. Hopefully sex specific behavioural differences provide another level of protection for species, through increased potential for rapid adaptation, against human induced environmental changes.

# Appendices

## Appendix 1

### The complementary error function

The complementary error function, erfc$[z]$, gives the area under the cumulative distribution curve. This is calculated as $1 - \text{erf}[z]$ where erf$[z]$ is the standard error of a normal distribution function;

$$\text{erfc}[z] = 1 - \text{erf}[z]$$

(Eqn 7.1)

$$= 1 - \frac{2}{\sqrt{\pi}} \int_0^z e^{-t^2}\, dt$$

(Eqn 7.2)

$$= \frac{2}{\sqrt{\pi}} \int_z^\infty e^{-t^2}\, dt$$

(Eqn 7.3)

Also:

$$\frac{\partial \text{erfc}[z]}{\partial z} = \frac{-2e^{-x^2}}{\sqrt{\pi}}$$

(Eqn 7.4)

(Weinstein, 2006c).

# Appendix 2

## Properties of the Gaussian function

To completely understand the model it is important to be aware of the properties of the probability density function (figure 7.1a and b); Changing the mean arrival date shifts the function left or right on the $x$-axis. Changing the standard deviation is more complicated as this affects the proportion of birds that arrive on each day. This can be examined by considering the height of the maxima, that is what proportion of the population arrive on the mean arrival date (figure 7.1c).

$$P(x = \mu) = \frac{1}{\sqrt{2\pi\sigma^2}} e^0 = \frac{1}{\sqrt{2\pi\sigma^2}}$$

(Eqn 7.5)

Where $\mu$ is the mean, $\sigma$ is the standard deviation and $x$ the individual measurement. The maxima occurs when $\mu = x$ (Kleckskowski, personal communication 2013):

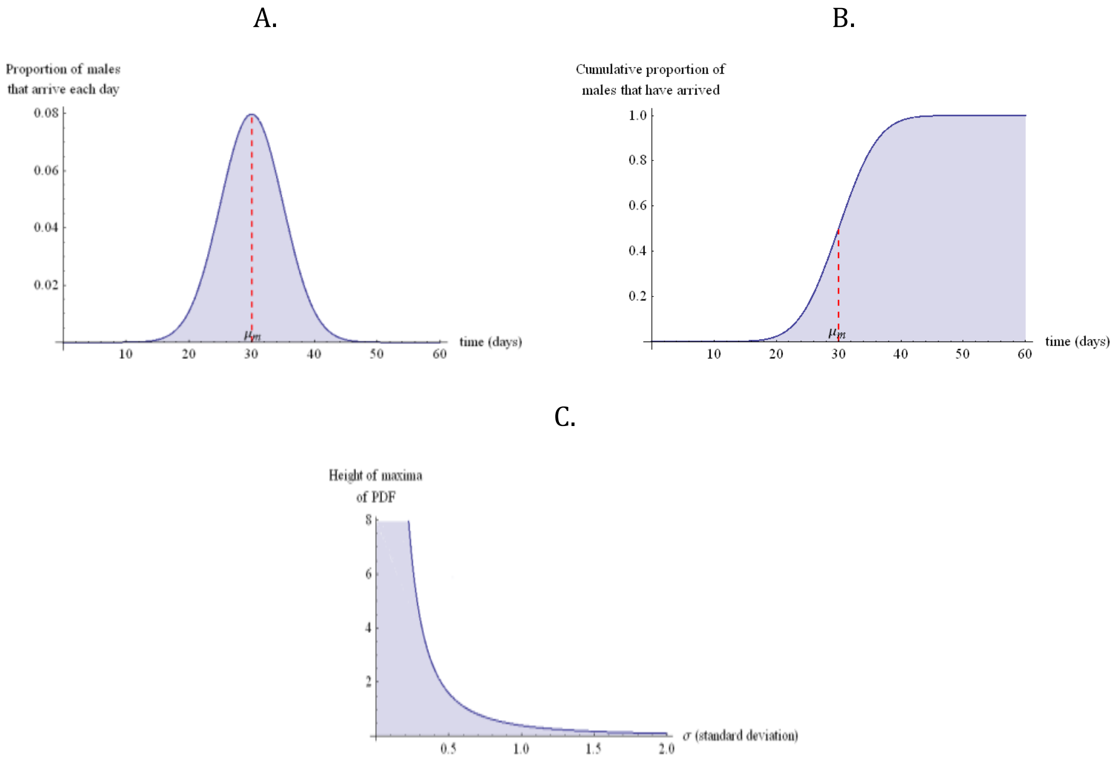

**Figure 7.1: The properties of the probability density function.**

- **A. The probability distribution function of male arrival dates.** The proportion of the male population that arrives on each day.
- **B. The cumulative distribution of male arrival dates.** The total proportion of the male population that arrives on each day.
- **C. Height of the probability density function maxima against standard deviation.** As the standard deviation increases the distribution becomes wider spread and the height of the maxima decreases.

# Appendix 3

## The length of the season change period

Changing $a$ and $b$ in the survival function $S(t)$ changes the slope and midpoint of the curve respectively. This changes where the change in season occurs from spring to winter and how long intermediate conditions occur. A range of $a$ out with [0,4] was considered biologically irrelevant. The survival function is a logistic curve so although it approaches 0 and 1 at either end of the function it only achieves them when $t = \pm\infty$, so at no point in the season is survival or death completely guaranteed. At points in the function that show the most obvious slope is when the most obvious changes in the season are occurring and winter is turning into spring. For low values of $a$ this period may last the entire season, for high values of $a$ it may only last a few days. To ease the understanding of the outputs and overlaps, cut-offs for survival are assumed; below $S(t) = 0.01$ assume death is guaranteed and above $S(t) = 0.99$ survival is guaranteed. The number of days between these two points, the changing phase of the season, varies according to $a$.

The length of the season change period is:

$$\frac{1}{1 + e^{-a(x-b)}} \in (0.01, 0.99)$$

(Eqn 7.6)

Let $b = 0$ and and $a$ be within [0,4].

This gives:

$$x_{upper} = -\frac{1}{a} ln\left(\frac{1}{0.01} - 1\right) + b$$

(Eqn 7.7)

and

$$x_{lower} = -\frac{1}{a} ln\left(\frac{1}{0.99} - 1\right) - b$$

(Eqn 7.8)

The actual length of the changing phase of the season is calculated with:

$$z = x_{upper} - x_{lower}$$

$$z = -\frac{1}{a} ln\left(\frac{1}{0.99} - 1\right) - b + \frac{1}{a} ln\left(\frac{1}{0.01} - 1\right) + b$$

(Eqn 7.9)

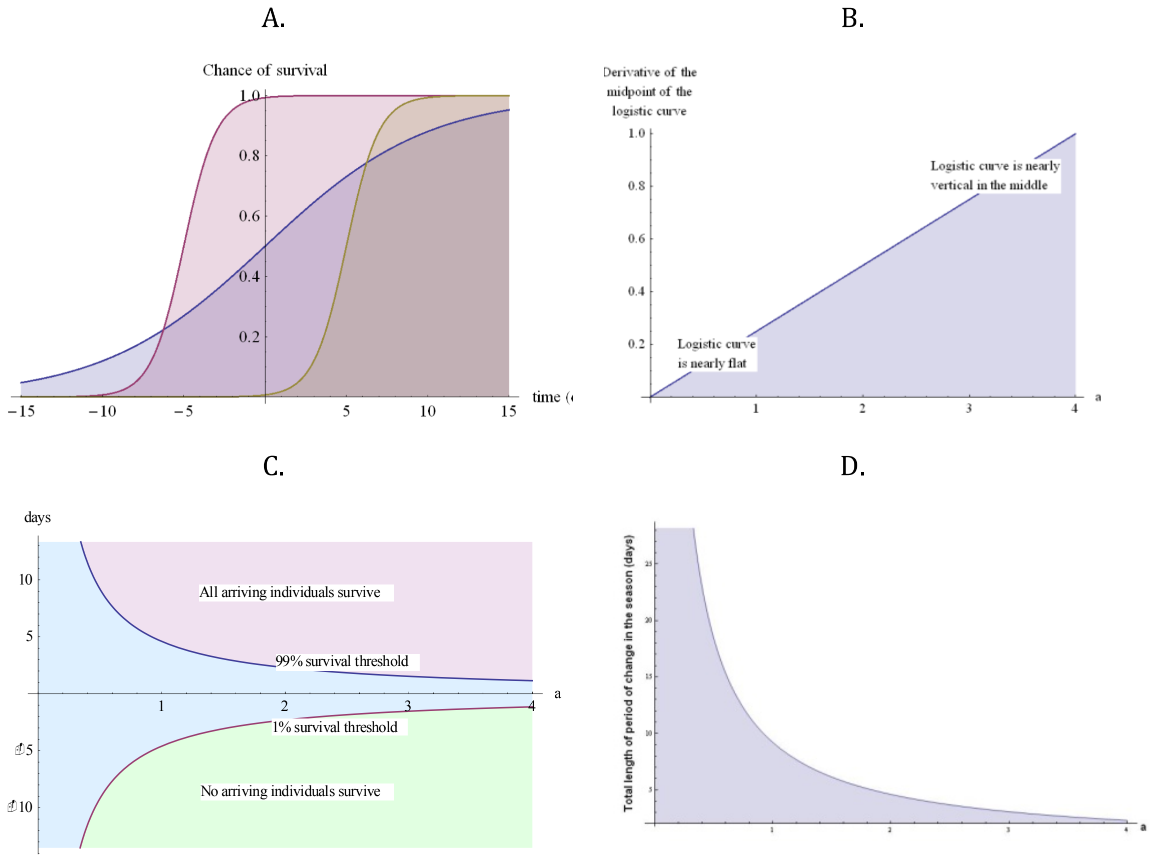

**Figure 7.2: The effects of changes to the parameters $a$ and $b$ on the survival curve $S(t)$ and the season.**

- **A. Different parameters may produce very different effects on the season.** This illustrates potential different forms that the logistic curve used to describe natural selection from environmental factors could take.
- **B. Increasing $a$ causes the survival curve to become steep.** This graph shows the gradient at the midpoint of the survival function for increasing values of $a$. Low values of $a$ produce a very long flat function, high values produce a much shorter, steeper function.
- **C. Contour plot of 99% and 1% survival thresholds and resulting length of time period of seasonal change.** The pink area indicates spring conditions where survival rates are high and the season change phase is complete, the green area indicates winter conditions where survival rates are low before the season change phase has begun. The green area indicates the season change phase where survival rates are variable.
- **D. The changing phase of the season gets shorter as $a$ increases.** This shows the size in days of the area of the blue segment from figure 7.1c.

# Appendix 4

## Example Fitness Equations

The figures here in appendix 4 illustrate example fitness curves for the final populations of each model as detailed in the results of chapter 2. For equal survival the parameters used are; $a_m = a_f = 0.1$ and $b_m = b_f = 90$. For male biased survival the parameters used are; $a_m = 1.0, a_f = 0.1$ and $b_m = 90, b_f = 110$. For female biased survival the parameters used are; $a_m = 0.1,\ a_f = 1.0$ and $b_m = 110, b_f = 90$.

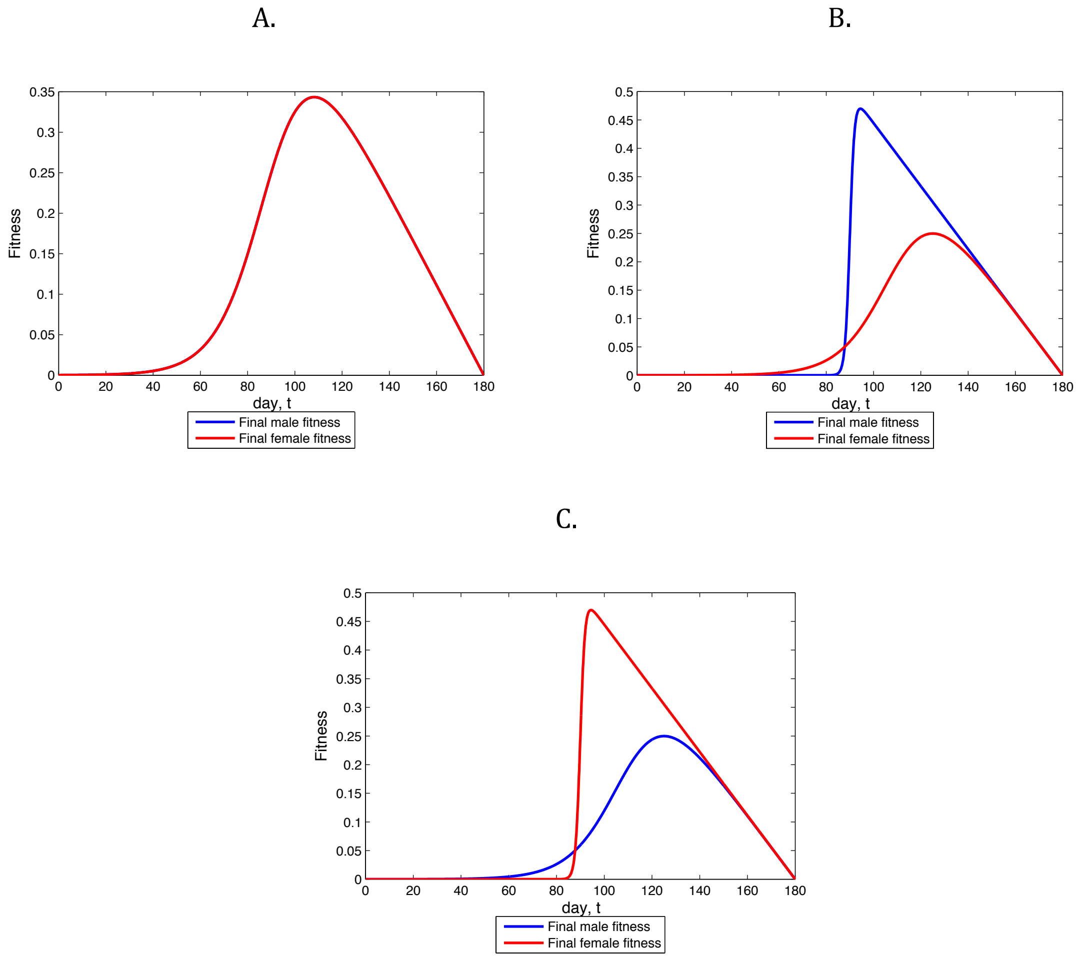

**Figure 7.3: Final population fitness curves from the environment model using less extreme parameter values.** These plots detail the fitness curves associated with the final populations illustrated in figure 2.9.

- **A. Assuming equal survival between males and females throughout the season results in equivalent fitness curves.** There is no difference for fitness achievable on each day of the season between males and females.
- **B. Male biased survival results in protandry.** Males achieve a maximum fitness earlier in the season than females.
- **C. Female biased survival results in protogyny.** Females achieve a maximum fitness earlier in the season than males.

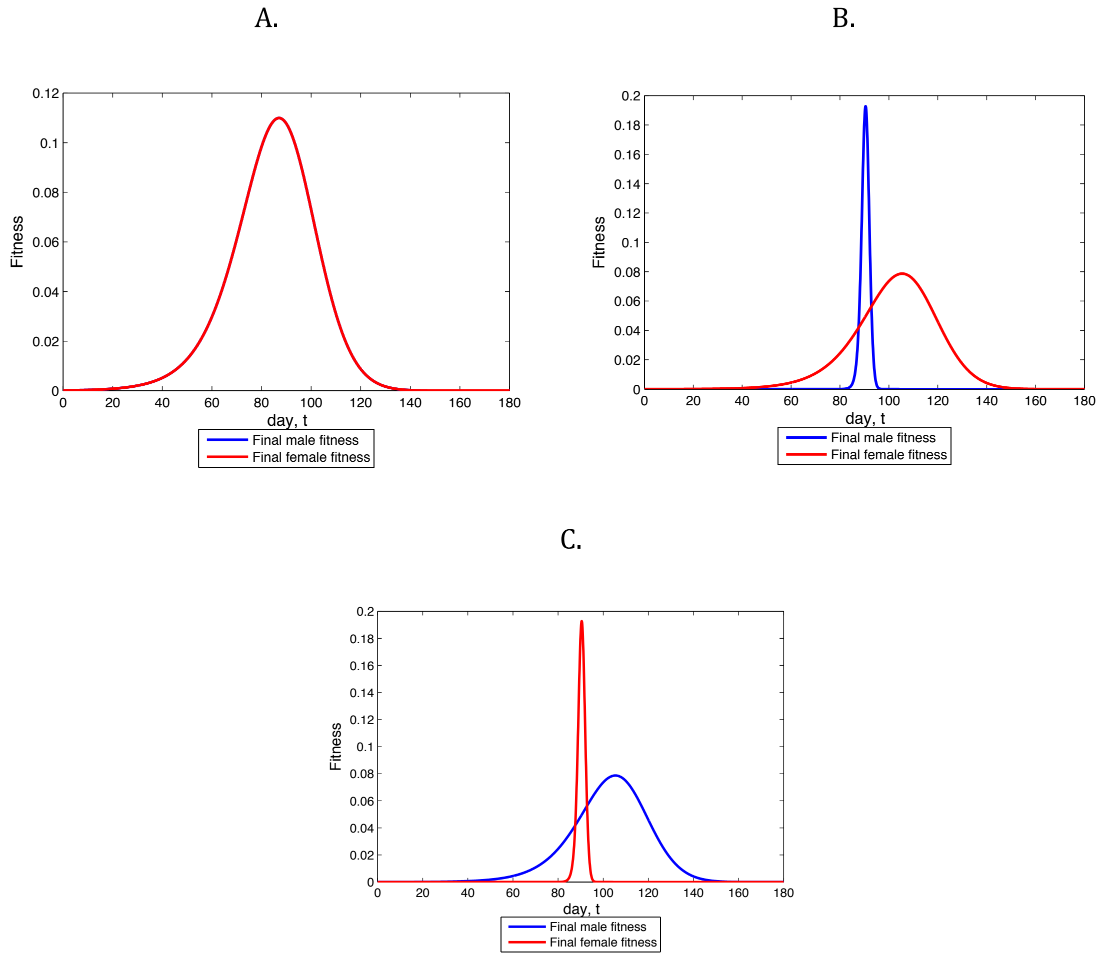

**Figure 7.4: Final population fitness curves from the rank advantage model using less extreme parameter values.** These plots detail the fitness curves associated with the final populations illustrated in figure 2.10.

**A.** **Assuming equal survival between males and females throughout the season results in equivalent fitness curves.** There is no difference for fitness achievable on each day of the season between males and females.

**B.** **Male biased survival results in protandry.** Males achieve a maximum fitness earlier in the season than females.

**C.** **Female biased survival results in protogyny.** Females achieve a maximum fitness earlier in the season than males.

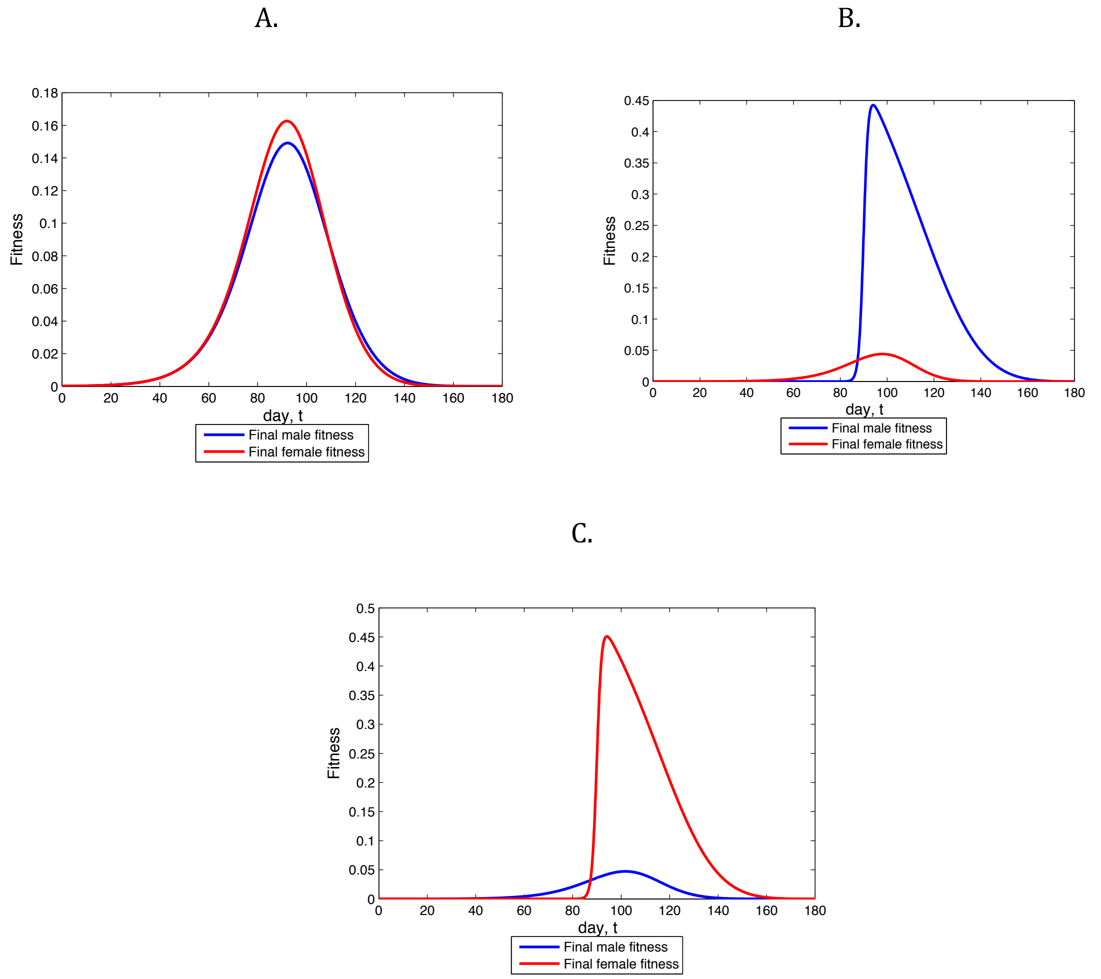

**Figure 7.5: Final population fitness curves from the mate opportunity model using less extreme parameter values.** These plots detail the fitness curves associated with the final populations illustrated in figure 2.11.

A. **Assuming equal survival between males and females results in neither true protandry nor protogyny.** Fitness curves reflect arrival curves in figure 2.11A.
B. **Male biased survival results in protandry.** Males achieve a maximum fitness earlier in the season than females.
C. **Female biased survival results in protogyny.** Females achieve a maximum fitness earlier in the season than males.

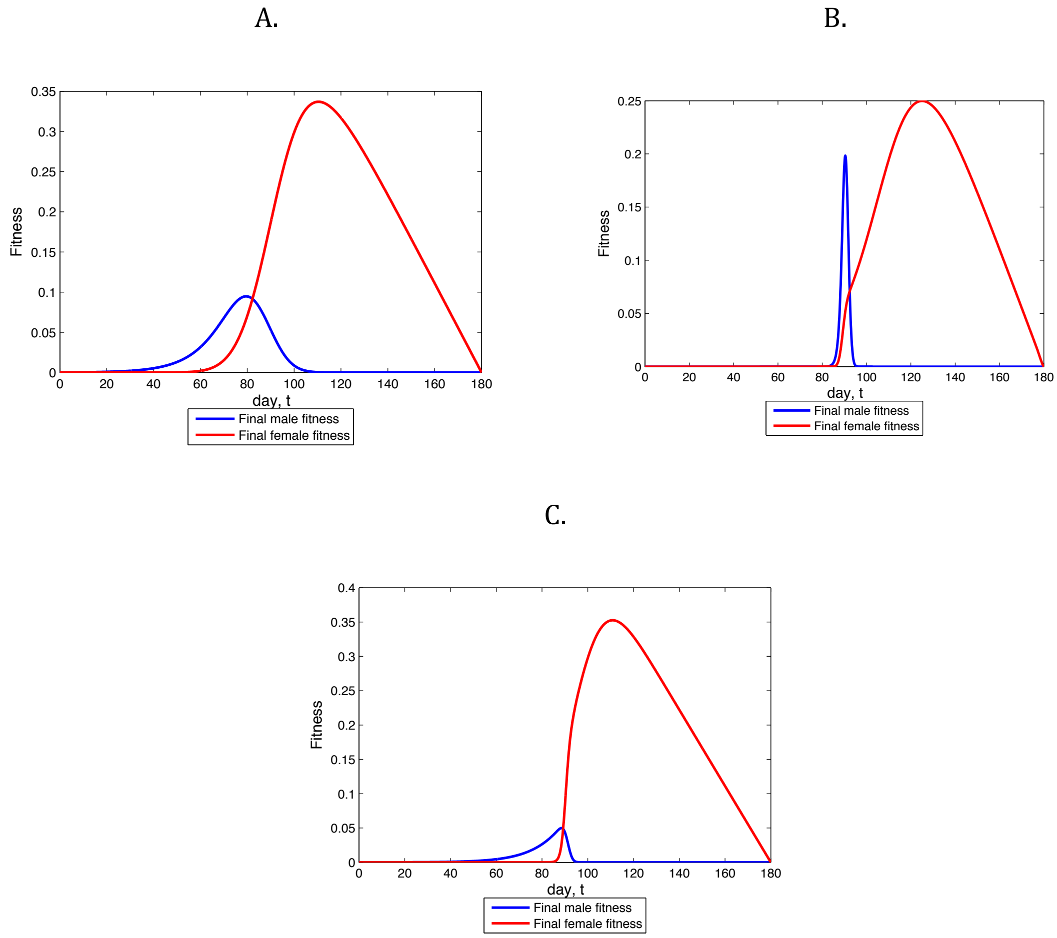

**Figure 7.6: Final population fitness curves from the integrated model using less extreme parameter values.** These plots detail the fitness curves associated with the final populations illustrated in figure 2.12.

- **A. Assuming equal survival between males and females protandry.** Male fitness peak is much earlier than female but females may achieve a much higher fitness relative to males at their peak.
- **B. Male biased survival results in protandry.** Male fitness peak is much earlier than female but females may achieve a much higher fitness relative to males at their peak. Maximum male fitness is much higher with a male sex bias than compared to when survival is equal between the sexes.
- **C. Female biased survival results in neither true protandry nor protogyny.** Male fitness peaks much earlier than females, but female maximum fitness is much higher than males.

# Appendix 5

## Reversal of female assumptions of the mate opportunity model

Kokko (2006) assumed females received a benefit of mating under the mate opportunity hypothesis due to increased chance for sperm competition and increased potential for EPC sired offspring. In the models in chapter 2, EPC sired young were considered a cost and thus mate opportunity was assumed to be costly to females. To test the effects of this assumption in the models of Chapter 2, the female function, $B_f(y)$, was reversed to $B_{f\_benefit}(y)$.

$$B_{f\_benefit}(y) = 1 - \frac{1}{2} erfc\left[\frac{\mu_m - y}{\sigma_m\sqrt{2}}\right]$$

(Eqn 7.10)

The model was rerun as detailed in Chapter 2 using $B_{f\_benefit}(y)$ in place of $B_f(y)$. When survival is equal the mate opportunity with female benefit model (using eqn 7.9) showed both sexes to arrive earlier than the female cost counterpart model and females to arrive two days before males (figure 7.3a). The results showed no difference between the two models when survival was male or female biased (figures 7.3b and 7.3c).

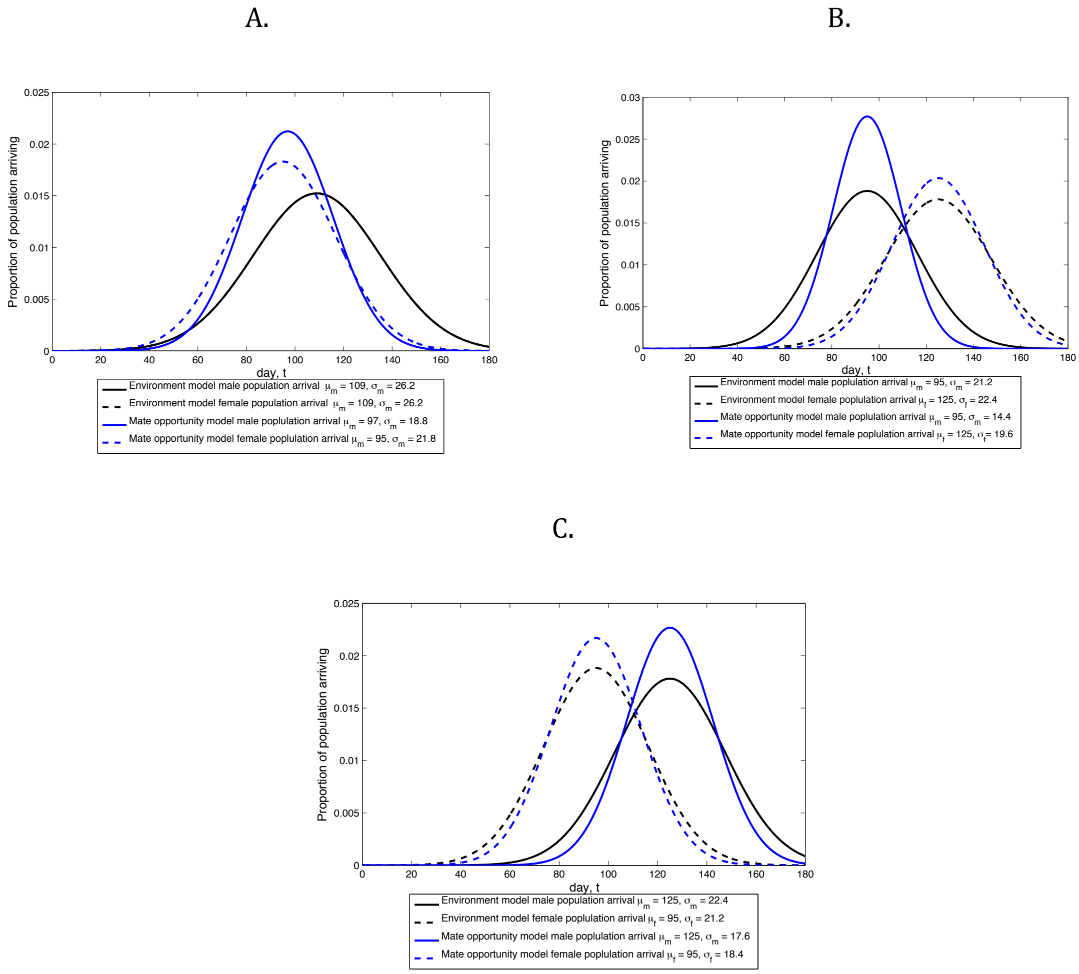

**Figure 7.7: The mate opportunity hypothesis assuming early arrival is beneficial to females.**

- **D. Equal environmental survival results in protogyny.** The population arrival date distributions are different to when female arrival is considered a cost (figure 2.11a). Here arrival of both sexes is advanced and females arrive earlier than males. Female arrival is slightly narrower and male arrival is slightly wider than when female arrival is considered a cost.
- **E. Male biased survival results in protandry.** The population arrival date distributions are exactly the same as when early female arrival was considered costly to females (figure 2.11b).
- **F. Female biased survival results in protogyny.** The population arrival date distributions are exactly the same as when early female arrival was considered costly to females (figure 2.11c).

# Appendix 6

## Partial derivatives of the protandry models using the canonical equation

### *Partial derivatives for the environmental model:*

$$\frac{\partial W_{M:Env}}{\partial x} = \frac{\partial S}{\partial x}L + S\frac{\partial L}{\partial x}$$

(Eqn 7.11)

$$\frac{\partial W_{F:Env}}{\partial y} = \frac{\partial S}{\partial y}L + S\frac{\partial L}{\partial y}$$

(Eqn 7.12)

### *Partial derivatives for the rank advantage hypothesis model:*

$$\frac{\partial W_{M:Rank}}{\partial x} = \frac{\partial S}{\partial x}LQ_M + S\frac{\partial L}{\partial x}Q_M + SL\frac{\partial Q_M}{\partial x}$$

(Eqn 7.13)

$$\frac{\partial W_{F:Rank}}{\partial y} = \frac{\partial S}{\partial y}LQ_F + S\frac{\partial L}{\partial y}Q_F + SL\frac{\partial Q_F}{\partial y}$$

(Eqn 7.14)

### *Partial derivatives for the Mate Opportunity Hypothesis Model:*

$$\frac{\partial W_{M:MateOp}}{\partial x} = \frac{\partial S}{\partial x}LB_M + S\frac{\partial L}{\partial x}B_M + SL\frac{\partial B_M}{\partial x}$$

(Eqn 7.15)

$$\frac{\partial W_{F:MateOp}}{\partial y} = \frac{\partial S}{\partial y}LB_F + S\frac{\partial L}{\partial y}B_F + SL\frac{\partial B_F}{\partial y}$$

(Eqn 7.16)

### *Partial derivatives for the integrated hypothesis model:*

$$\frac{\partial W_{M:Int}}{\partial x} = \frac{\partial S}{\partial x}Q_M B_M L + S\frac{\partial Q_M}{\partial x}B_M L + SQ_M\frac{\partial B_M}{\partial x}L + SQ_M B_M\frac{\partial L}{\partial x}$$

(Eqn 7.17)

$$\frac{\partial W_{F:Int}}{\partial y} = \frac{\partial S}{\partial y}Q_F B_F L + S\frac{\partial Q_F}{\partial y}B_F L + SQ_F\frac{\partial B_F}{\partial y}L + SQ_F B_F\frac{\partial L}{\partial y}$$

(Eqn 7.18)

### *Partial derivative subsidiaries*

$$\frac{\partial S}{\partial t} = \frac{ae^{-a(t-b)}}{(1+e^{-a(t-b)})^2}$$

(Eqn 7.19)

$$\frac{\partial L}{\partial t} = 1 - \frac{1}{180}$$

(Eqn 7.20)

$$\frac{\partial Q}{\partial t} = -\frac{0.398942e^{\frac{-(\mu - t)}{2\sigma^2}}}{\sigma}$$

(Eqn 7.21)

$$\frac{\partial B_M}{\partial x} = -\frac{0.398942e^{\frac{-(\mu_F - x)}{2\sigma_F{}^2}}}{\sigma_F}$$

(Eqn 7.22)

$$\frac{\partial B_F}{\partial y} = \frac{0.398942e^{\frac{-(\mu_M - y)}{2\sigma_M{}^2}}}{\sigma_M}$$

(Eqn 7.23)

Where $t$ may be either male or female arrival day as appropriate.

# Appendix 7

## Utilisation of MatLab

MatLab was used to code all models and the following is an example of the program used to allow mean arrival date and population distribution width of male and female birds in the environment model of protandry.

```
% Pre-amble
clear all;
aM = 0.1; % male survival function slope
aF = 0.1; % female survival function slope
bM = 135; % male survival function midpoint
bF = 135; % male survival function midpoint
LM = 180; % male season length
LF = 180; % female season length
sdM(1) = 3; % male initial standard deviation
sdF(1) = 3; % female initial standard deviation
muM(1)=25; % male initial mean arrival date
muF(1)=25; % female initial mean arrival date

tval=-179:1:360;
n=300;
  for i=1:n;
    x=muM(i);
    y=muF(i);
    % Environmental survival function and partial derivatives
    environmental_survival_Male = (1/(1 + exp(-aM*(x - bM))));
    d_environmental_survival_Male_x = (aM*exp(-aM*(x - bM)))/((1 + exp(-aM*(x - bM))).^2);
    environmental_survival_Female = (1/(1 + exp(-aF*(y - bF))));
    d_environmental_survival_Female_y = (aF*exp(-aF*(y - bF)))/((1 + exp(-aF*(y-bF))).^2);

    % Time to rear offsprting function and partial derivatives
    Season_End_Male = (1-(1/LM)*x);
    d_Season_End_Male_x = (-1/LM);
    Season_End_Female = (1-(1/LF)*y);
    d_Season_End_Female_y = (-1/LM);

   % Partial derivatives of the fitness equations
    dWm_dx_BASELINE = d_environmental_survival_Male_x * Season_End_Male +... environmental_survival_Male  *
d_Season_End_Male_x;
    dWf_dy_BASELINE = d_environmental_survival_Female_y * Season_End_Female +... environmental_survival_Female *
d_Season_End_Female_y;

   % Adjust the average arrival date of the nth generation according to the fitness gradient of the n-1th generation
    muM(i+1)=muM(i)+ sign(dWm_dx_BASELINE)*1;
    muF(i+1)=muF(i)+ sign(dWf_dy_BASELINE)*1;

    % Calculate the width of the fitness curves
    for ival=1:540;
      Season_End_Male_ival = (1-(1/LM)*(ival-180));
      Season_End_Female_ival = (1-(1/LF)*(ival-180));
      environmental_survival_Female_ival = (1/(1 + exp(-aF*((ival-180) - bF))));
      environmental_survival_Male_ival = (1/(1 + exp(-aM*((ival-180) - bM))));
      Wm_BASELINE(ival) = environmental_survival_Male_ival * Season_End_Male_ival ;
      if Wm_BASELINE(ival) <0;
        Wm_BASELINE(ival) = 0;
      end
      Wf_BASELINE(ival) = environmental_survival_Female_ival * Season_End_Female_ival ;
      if Wf_BASELINE(ival) <0;
        Wf_BASELINE(ival) = 0;
      end
    end
    % Standardize the fitness curve to make widths comparable
    for ival=1:540;
      Wm_norm(ival)=  Wm_BASELINE(ival)/sum(Wm_BASELINE(:));
      Wf_norm(ival)=  Wf_BASELINE(ival)/sum(Wf_BASELINE(:));
    end
    % adjust the nth generation population standard deviation according to the width of the fitness curve
    Fit_sd_m(i) = (sum(Wm_norm(:).*tval(:).^2) - (sum(Wm_norm(:).*tval(:)))^2)^0.5;
    sdM(i+1)    = sdM(i)+ sign(Fit_sd_m(i) - sdM(i))*0.1;
    Fit_sd_f(i) = (sum(Wf_norm(:).*tval(:).^2) - (sum(Wf_norm(:).*tval(:)))^2)^0.5;
    sdF(i+1)    = sdF(i)+ sign(Fit_sd_f(i) - sdF(i))*0.1;
  end
```

# Appendix 8

## Further results of chapter 2

Initially the models of Chapter 2 were tested assuming extreme sets of parameters for male biased and female biased survival (figure 7.4). For equal survival these parameters are; $a_m = a_f = 0.1$ and $b_m = b_f = 90$. For male biased survival these parameters are; $a_m = 1.0, a_f = 0.1$ and $b_m = 60, b_f = 135$. For female biased survival these parameters are; $a_m = 0.1$, $a_f = 1.0$ and $b_m = 135, b_f = 60$. Results were achieved in the same manner as those detailed in Chapter 2 and are summarised in figures 7.5- 7.9.

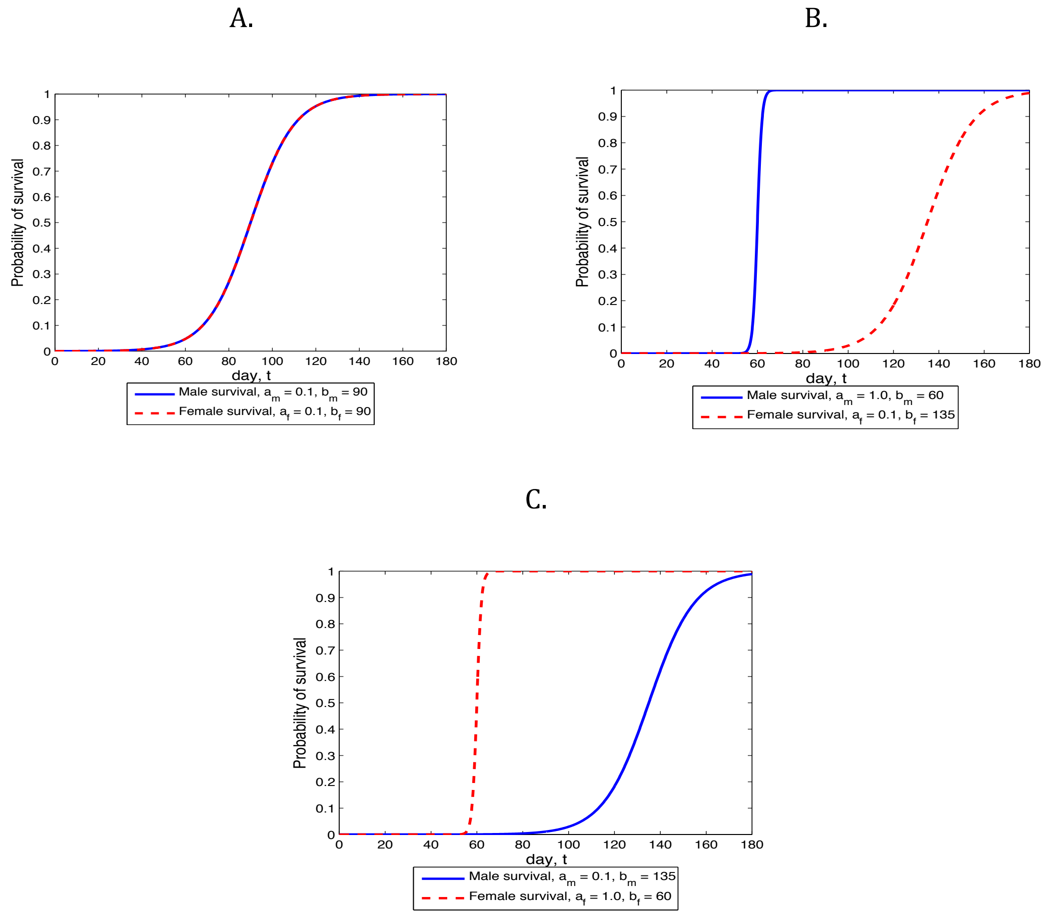

**Figure 7.8: Models were tested under 3 different sets of extreme conditions.**

- **A.** **Equal conditions of survival.** Both *a* and *b* parameters are equal for males and females and set at an intermediate value.
- **B.** **Extremely male biased survival.** Males have a higher *a* value and a lower *b* value than females.
- **C.** **Extremely female biased survival.** Females have a higher *a* value and a lower *b* value than males.

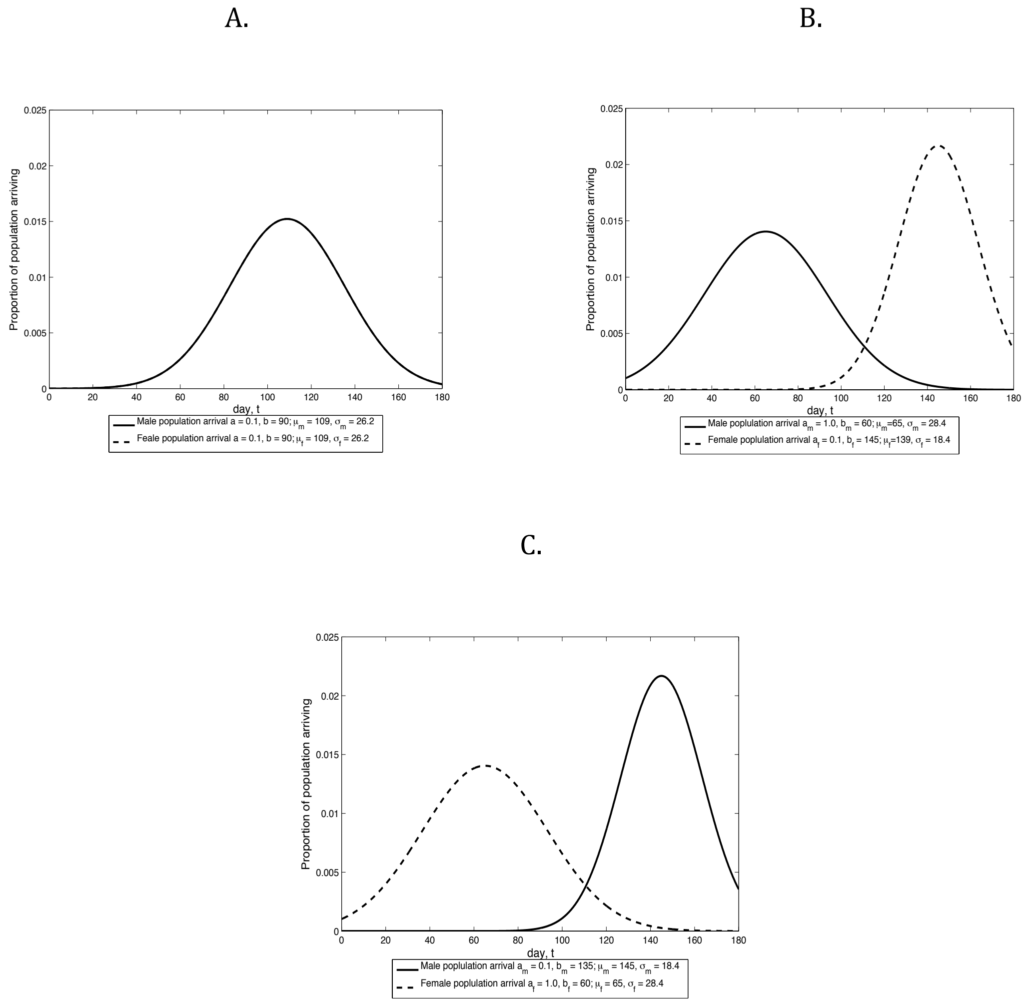

**Figure 7.9: Results of the environmental model under extreme condition sets**

A. **Equal environmental survival conditions result in neither protandry nor protandry.** When conditions are equal for both sexes and females evolve to arrive on the same day with equal distributions. Final value of male and female mean arrival and standard distributions are detailed in the legend.

B. **Male biased survival results in protandry.** When conditions favour early male arrival and late female arrival, protandry evolves.

C. **Female biased survival results in protogyny.** When conditions favour early female arrival, protogyny evolves. The population distributions for female biased survival are the reverse of those that evolved under male biased survival.

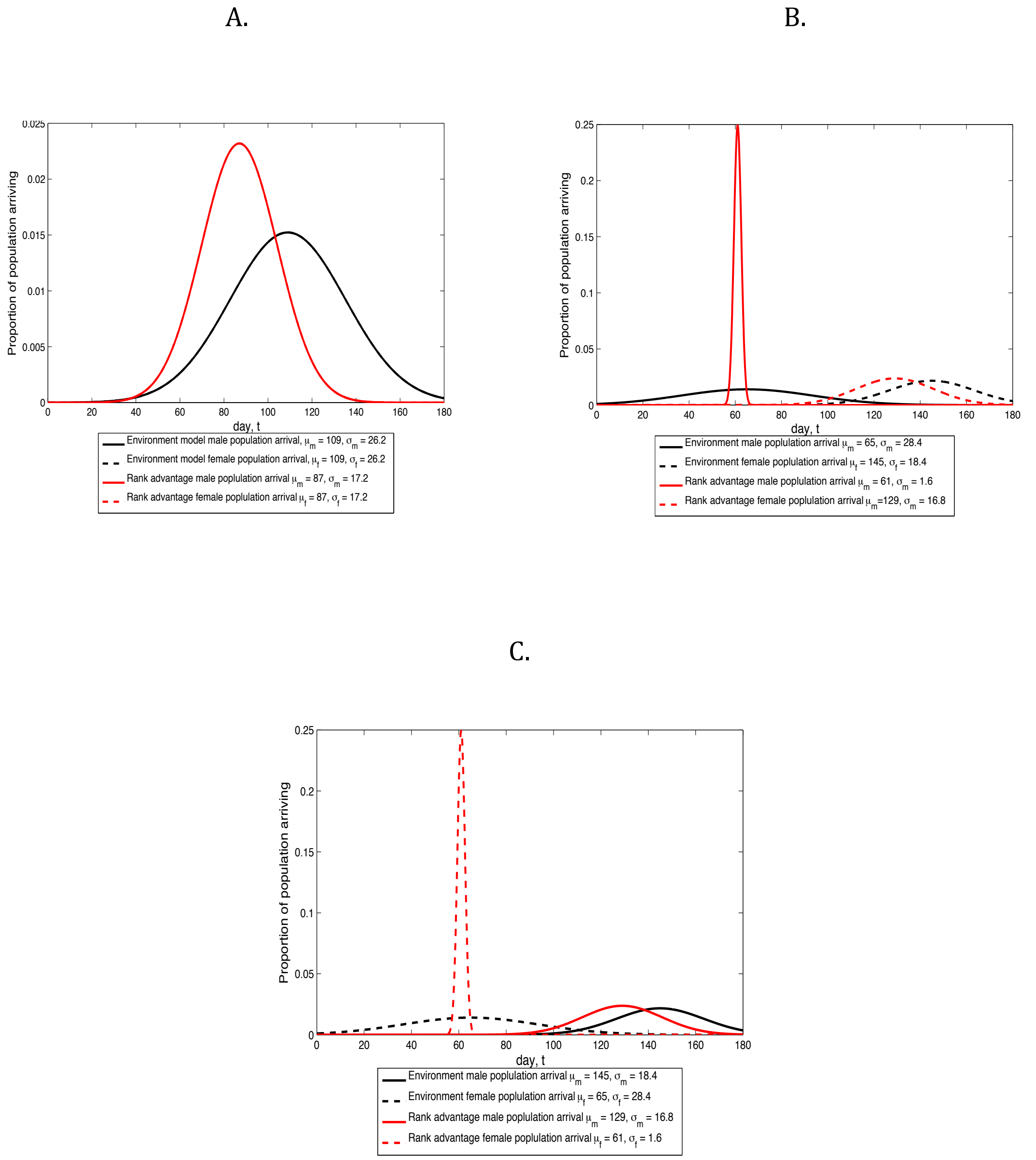

**Figure 7.10: Results of the rank advantage model under extreme condition sets**

A. **Equal environmental survival conditions results in neither protandry nor protogyny.** With no survival differences both sexes arrive with equal distributions. The populations arrive earlier and with a narrower distribution than the environment model.
B. **Male biased survival results in protandry.** Protandry persists when survival is male biased. Male arrival distribution is much narrower than the environment model and mean arrival is earlier for both male and female populations than the environment model.
C. **Female biased survival results in protogyny.** A large degree of protogyny is evident and distributions are the exact reverse of those seen under male biased survival.

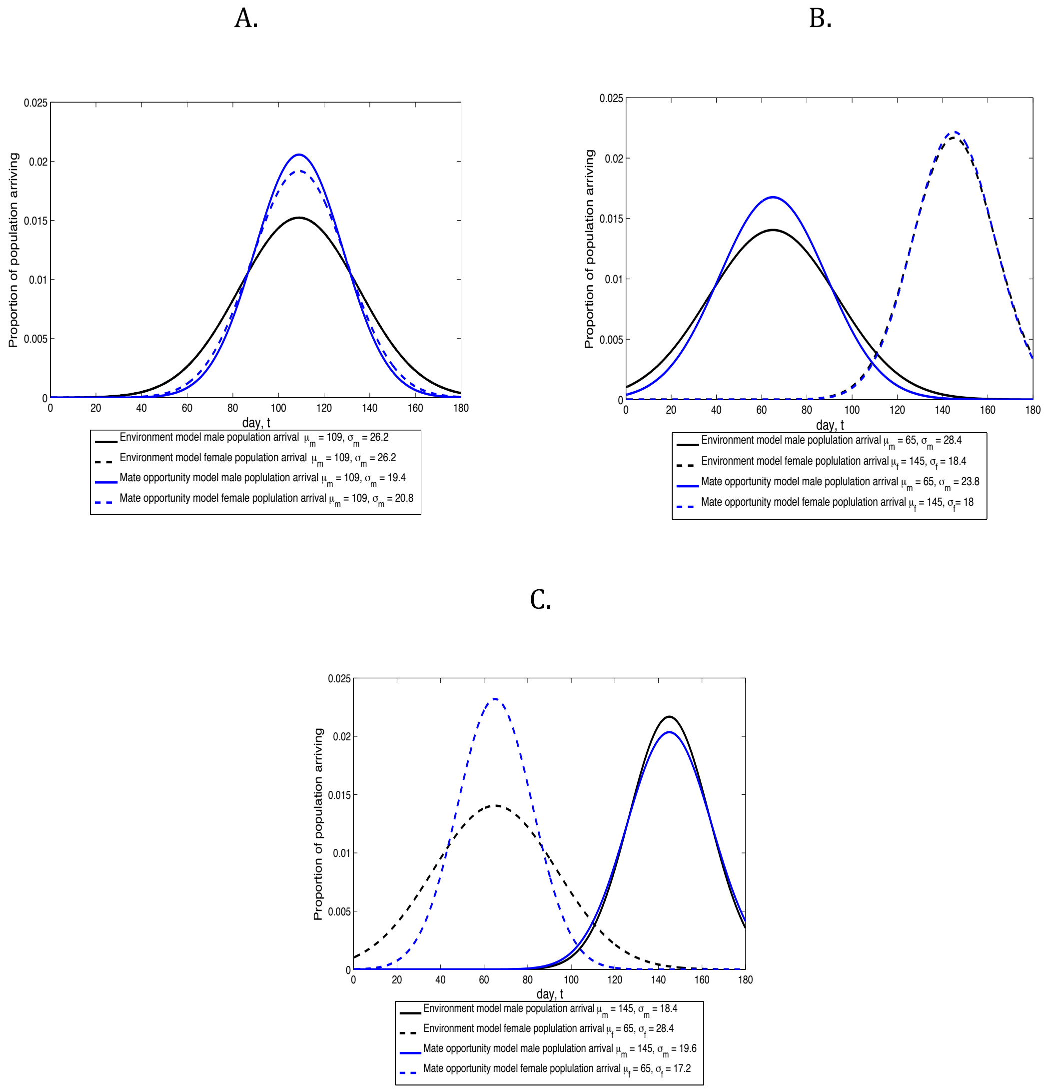

**Figure 7.11: Results of the mate opportunity model under extreme condition sets**

**A. Equal environmental survival conditions results in no difference between male and female mean arrivals.** With no survival bias the populations evolve equal mean arrival dates but female population is slightly more widely distributed than male so the very first females arrive just before the very first males. Both population's distributions are narrower than the environmental model however.

**B. Male biased survival results in protandry.** Protandry persists when survival is male biased and the degree is increased. Male population arrives earlier than the environmental model and female later. The male population has a narrower distribution and the female a wider distribution than the control.

**C. Female biased survival results in no difference between male and female mean arrivals.** The mean arrival dates of both populations are equal and at an intermediate value between the male and female mean arrivals of the environmental population. Slight protogyny occurs because the female distribution is slightly wider than the male distribution.

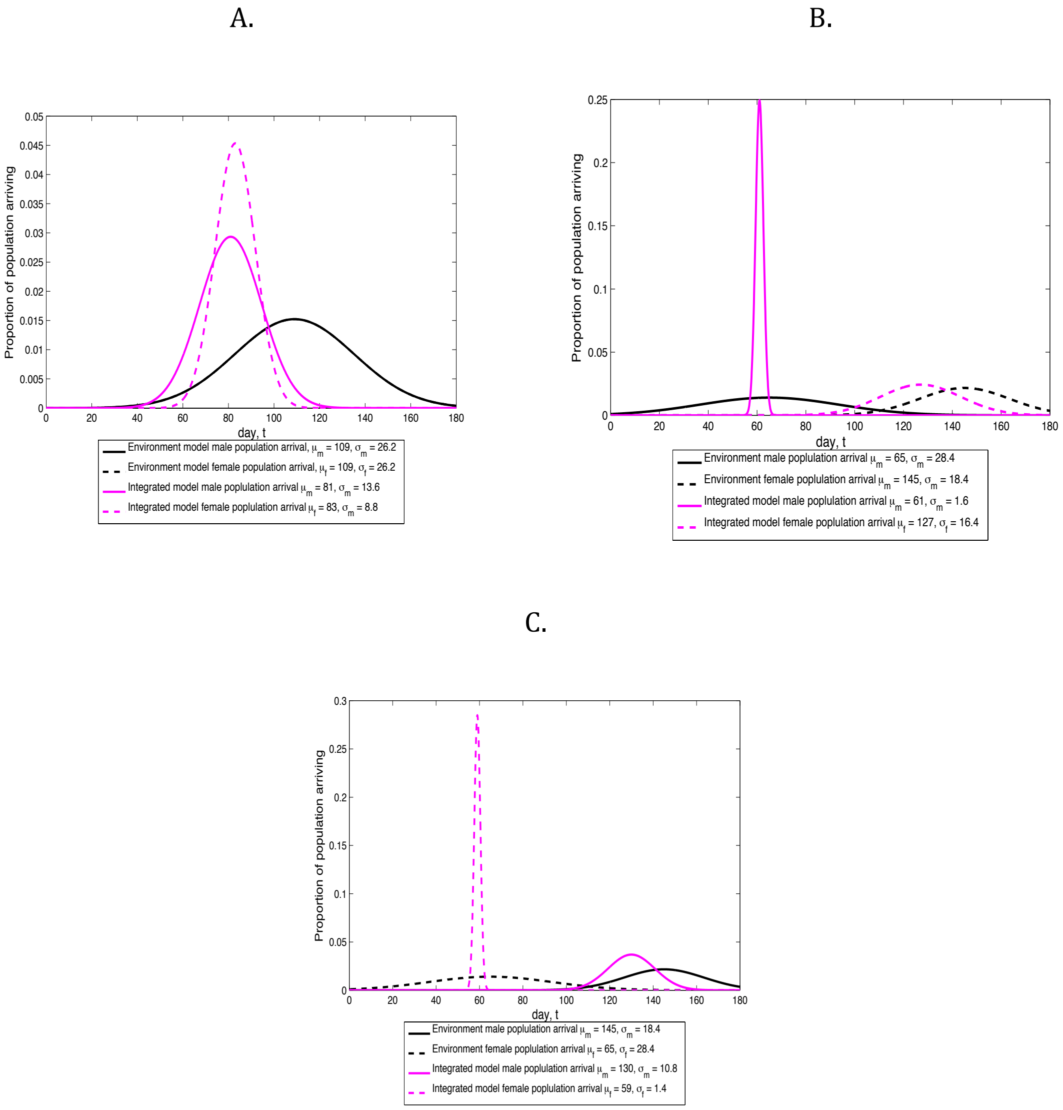

**Figure 7.12: Results of the integrated model under extreme condition sets**

**D.** **Equal environmental survival conditions results in slight protandry.** With no survival bias the populations evolve equal mean arrival dates but male population is more widely distributed than male so the very first males arrive just before the very first females. Both population's distributions are narrower than the environmental model however and arrival is much earlier.

**E.** **Male biased survival results in protandry.** Both populations evolve to arrive earlier than the environmental model and with a narrower distribution. The female distribution is very narrow.

**F.** **Female biased survival results in neither protandry nor protogyny.** The mean arrival dates and standard distributions of both populations are equal. Mean arrival date is considerably advanced compared to environment model.

# Appendix 9

## Summary of the equations and functions of the protandry models in Chapter 2

The models and construction process are detailed fully in chapter 2 but are summarised here for reference. All models include a survival term and a decreasing egg-laying potential (Eqn. 9 & 10) as a basis. The rank advantage model includes functions relating decreasing territory quality to lateness in arrival time in both sexes. The mate opportunity model considers increasing male opportunity to mate with early arrival relative to female arrival and increasing avoidance of female costs with late arrival relative to male arrival (Eqn. 12 & 13).

Environment model:

$$W_{Male:Environment} = s_m(x) \times L(x)$$

(Eqn 7.24)

$$W_{Female:Environment} = s_f(y) \times L(y)$$

(Eqn 7.25)

Rank advantage model:

$$W_{Male:Rank} = S_m(x) \times L(x) \times Q_m(x)$$

(Eqn 7.26)

$$W_{Female:Rank} = S_f(y) \times L(y) \times Q_f(y)$$

(Eqn 7.27)

Mate opportunity model:

$$W_{Male:MateOp} = S_m(x) \times L(x) \times B_m(x)$$

(Eqn 7.28)

$$W_{Female:MateOp} = S_f(y) \times L(y) \times B_f(y)$$

(Eqn 7.23)

Integrated model of rank advantage and mate opportunity:

$$W_{Male:Integrated} = S_m(x) \times Q_m(x) \times B_m(x) \times L(x)$$

(Eqn 7.30)

$$W_{Female:Integrated} = S_f(y) \times Q_f(y) \times B_f(y) \times L(y)$$

(Eqn 7.31)

The components of the models are now summarised where $x$ is male arrival date, $y$ is female arrival date and $t$ is general arrival date applicable to either sex:

$$s(t) = \frac{1}{1 + e^{-a(t-b)}}$$

(Eqn 7.32)

$$L(t) = 1 - \frac{t}{180}$$

(Eqn 7.33)

$$Q(t) = 1 - \frac{1}{2} \operatorname{erfc}\left[\frac{\mu - t}{\sigma\sqrt{2}}\right]$$

(Eqn 7.34)

$$B_m(x) = -\frac{1}{2} erfc\left[\frac{\mu_f - x}{\sigma_f\sqrt{2}}\right]$$

(Eqn 7.35)

$$B_f(y) = \frac{1}{2} erfc\left[\frac{\mu_m - y}{\sigma_m\sqrt{2}}\right]$$

(Eqn 7.36)

# Appendix 10

## Partial derivatives of the convenience polyandry model using the canonical equation

From the fitness equations we gain the evolutionary dynamics of male size, $x$, female response sensitivity, $s$, and female response threshold, $T$, using standard method of the canonical equation derived from adaptive dynamic techniques (Iwasa et al. 1991; Dieckmann & Law, 1996; Abrams et al. 2001) to give the change in male fitness with respect to size:

$$\frac{\partial W_M}{\partial x} = \beta\gamma_A\frac{\partial\alpha}{\partial x} + (1-\beta)\left(\gamma_F\frac{\partial\alpha}{\partial x} + \alpha\frac{\partial\gamma_F}{\partial x}\right) + \alpha\left(\frac{\partial\beta}{\partial x}(\gamma_A-\gamma_F) + \beta\frac{\partial\gamma_A}{\partial x}\right)$$

(Eqn 7.37)

The change in female fitness with respect to response sensitivity;

$$\frac{\partial W_F}{\partial s} = \frac{Z_C\frac{\partial Z_M}{\partial s} - Z_M\frac{\partial Z_C}{\partial s}}{{Z_C}^2}$$

(Eqn 7.38)

And with respect to response threshold;

$$\frac{\partial W_F}{\partial T} = \frac{Z_C\frac{\partial Z_M}{\partial T} - Z_M\frac{\partial Z_C}{\partial T}}{{Z_C}^2}$$

(Eqn 7.39)

Where;

$$\frac{\partial Z_M}{\partial s} = \alpha\frac{\partial\beta}{\partial s}(\gamma_A-\gamma_F)$$

(Eqn 7.40)

$$\frac{\partial Z_M}{\partial T} = \alpha\frac{\partial\beta}{\partial T}(\gamma_A-\gamma_F)$$

(Eqn 7.41)

And;

$$\frac{\partial Z_C}{\partial s} = \alpha \frac{\partial \beta}{\partial s}\big(\theta_A - \theta_F + \mu(\gamma_A - \gamma_F)\big)$$

(Eqn 7.42)

$$\frac{\partial Z_C}{\partial T} = \alpha \frac{\partial \beta}{\partial T}\big(\theta_A - \theta_F + \mu(\gamma_A - \gamma_F)\big)$$

(Eqn 7.43)

# Appendix 11

## The effect of seaweed species on egg-laying in *C. frigida*

### *Methods*

The aim is to investigate the effect different seaweed types have on egg laying of *C. frigida*. Forty virgin female *C. frigida* were paired individually with between 1 and 5 males and given a ball of cotton wool dipped in sucrose plus either 15g of fresh minced Laminaria or 15 g of fresh minced Ascophyllum seaweed. Flies were left until death which occurred approximately 4 days later. After natural parental death the number of clutches of eggs laid and the number of eggs (including any hatched eggs) in each clutch was recorded. To analyse the results, MiniTab was used to test for correlations between the number of eggs in each clutch, the number of eggs laid and the number of clutches laid with the number of males the female had been exposed to. Two sample t-tests were also conducted between mean number of eggs and mean number of clutches against seaweed type.

### *Results*

For females exposed to between 1 and 5 males there was no significant correlation between female survival and exposure to multiple males, total eggs laid, number of clutches nor number of eggs in each clutch (Table 6.1), however every *r* value was negative. There was a significant difference between the mean numbers of eggs laid on each type of seaweed, with Ascophyllum having a considerably higher mean than Laminaria (Table 7.1)

**Table 7.1: 2 sample t-test of seaweed species and egg count in *C. frigida*.** There is a significant difference between eggs laid on each type of seaweed.

| | 2 sample t-test | | | |
|---|---|---|---|---|
| Seaweed Species | **Mean** | **St. Dev** | **d.f.** | **P-Value** |
| *Ascophyllum* | 21.4 | 9.74 | 7 | 0.039 |
| *Laminaria* | 6.8 | 10.9 | | |

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‘It is not the mountain we conquer, only ourselves.’