

# Why do female migratory birds arrive later than males?

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## Summary

1. In migratory birds males tend to arrive first on breeding grounds, except in sex-role reversed species. The two most common explanations are the rank advantage hypothesis, in which male–male competition for breeding sites drives stronger selection for early arrival in males than females, and the mate opportunity hypothesis, which relies on sexual selection, as early arrival improves prospects of mate acquisition more for males than for females.
2. To date, theoretical work has focused on selection for early arrival within a single sex, usually male. However, if fitness depends on territory quality, selection for early arrival should operate on both sexes. Here we use two independent modelling approaches to explore the evolution of protandry (male-first arrival) and protogyny (female-first arrival) under the rank advantage and mate opportunity hypotheses.
3. The rank advantage hypothesis, when operating alone, fails to produce consistent patterns of protandry, despite our assumption that males must occupy territories before females. This is because an individual of either sex benefits if it out-competes same-sex competitors. Rather than promoting protandry, the rank advantage mechanism can sometimes result in protogyny. Female–female competition is stronger than male–male competition early in the season, if females compete for a resource (territories occupied by males) that is initially less common than the resource of interest to males (unoccupied territories).
4. Our results support the mate opportunity hypothesis as an explanation of why protandry is the norm in migratory systems. Male-biased adult sex ratios and high levels of sperm competition (modelled as extra-pair young: EPY) both produce protandry as a result of sexual selection. Protogyny is only observed in our models with female-biased sex ratios and low EPY production.
5. We also show that the effects of sex ratio biases are much stronger than those of EPY production, explore the evidence for sex ratio biases and extra-pair paternity in migratory species and suggest future research directions.

**Key-words:** arrival timing, extra-pair fertilization, population sex ratio, sex-role reversal, territoriality.

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## Introduction

Protandry refers to earlier arrival of males than females (Morbey & Ydenberg 2001). Here ‘arrival’ may broadly

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mean completion of a migratory journey (Myers 1981), production of offspring of different sexes (Kranz *et al.* 1999), emergence from a developmental stage (Fagerström & Wiklund 1982) or other similar processes. Protandry is found widely in migratory birds, while its opposite – protogyny, earlier arrival of females – has been found in only a few sex-role-reversed bird species (Oring & Lank 1982; Reynolds, Colwell & Cooke 1986).

In their review of seven different hypotheses to explain protandry in various taxa, Morbey & Ydenberg (2001)

state that two have become accepted for migratory birds. The hypothesis with the strongest support so far for migratory, territorial birds is the rank advantage hypothesis (*sensu* Morbey & Ydenberg 2001). This hypothesis is based on the benefits of gaining priority access to territories. If early males obtain superior territories selection will advance arrival dates, in some cases up to quite risky periods in the year (Kokko 1999). Using the terminology of Morbey & Ydenberg (2001), selection for protandry is indirect under this hypothesis. The arrival times of the two sexes evolve independently and protandry is a consequence of stronger selection on early arrival in males than in females.

The mate opportunity hypothesis (*sensu* Morbey & Ydenberg 2001) also has some support in the ornithological literature. This hypothesis has its roots in studies of insect emergence times, and has attracted substantial attention by theoreticians. Female fitness depends typically on the number of matings less strongly than male fitness (Andersson 1994). If males arrived simultaneously with females (but with some variation around the mean), individual males would lose mating opportunities as they cannot mate with females who are receptive before the male has arrived or emerged (Fagerström & Wiklund 1982; Bulmer 1983; Iwasa *et al.* 1983; Morbey 2002). Thus males arrive earlier. Morbey & Ydenberg (2001) classify the mate opportunity hypothesis as a direct selective advantage, the relative timing of male and female arrival being directly under selection.

Morbey & Ydenberg (2001) point out that the hypotheses for protandry in birds are not mutually exclusive, that future modelling work would benefit from considering multiple selective pressures simultaneously and that theoretical work has concentrated mainly on the mate opportunity hypothesis. The problem is particularly severe for studies of migratory birds, where the rank advantage hypothesis is widely believed to be appropriate. Morbey & Ydenberg (2001) cite Kokko (1999) for providing the theoretical backbone for the rank advantage hypothesis, yet the model by Kokko (1999) does not consider the difference between male and female arrival times. Instead, it includes only competition within a single sex, usually interpreted as males. However, female fitness will suffer similarly if late arrival forces females to occupy poor quality breeding sites (Bensch & Hasselquist 1991), thus both sexes should arrive early to occupy the best territories (Smith & Moore 2005). No theoretical work to date explicitly predicts arrival time differences based on the rank advantage hypothesis.

The goal of the current paper is to fill in this gap and to model multiple selective pressures. We employ two different methods with slightly different assumptions and research foci. Modelling results become considerably more robust if similar conclusions can be drawn from two completely different approaches. The models allow us to assess the prospects for protandry when the rank advantage hypothesis is operating alone, or together with processes that relate to the mate opportunity hypothesis,

such as biased adult sex ratios or extra-pair paternity that leads to sperm competition.

## MODELLING ARRIVAL TIMES OF MIGRATORY BIRDS

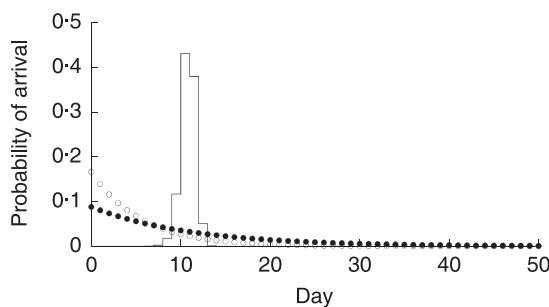
We present first a simplified numerical analysis, then proceed to an individual-based simulation. Any modelling method has advantages and drawbacks (Levins 1966). In our particular case, an individual-based simulation allows more flexibility and thus heightened biological realism, but it also has the unavoidable drawback that precise conclusions – such as determining the exact direction of protandry vs. protogyny when differences in arrival times are small – are hard to achieve (e.g. Lomnicki 1999). It is therefore good practice to begin with a simpler modelling technique to expose the logic of an argument. In both models a bird's strategy is its 'target' arrival date, denoted  $t$ , and small values of  $t$  indicate that the bird arrives early, on average. Also, in both models no bird can decide on an exact arrival date because chance events such as adverse weather conditions or other environmental factors can cause delays.

### MODEL 1. NUMERICAL ANALYSIS OF QUALITY-DEPENDENT ARRIVAL TIMES

In our first model, we derive predictions for a population consisting of four different types of individuals: in addition to being male or female, individuals of either sex are also of high or low quality. We also divide territories into two quality categories: good and poor. The model tracks changes in numbers of birds on each day from  $d = 0$  to  $d = D$ , including deaths, and calculates the expected numbers of individuals in each category that result in one of 16 (for males) or 12 (for females) different states (Appendix I). The reason for a different number of states for the two sexes is a sexual difference in territory acquisition behaviour: only males can occupy a territory without yet having found a mate. Therefore, for example, the state 'low quality male on a poor territory without a female' is possible, while females cannot have a territory without a mate.

Prior to the onset of spring migration, there are  $n_{M1}$ ,  $n_{M0}$ ,  $n_{F1}$  and  $n_{F0}$  individuals (high- and low-quality males, high- and low-quality females, respectively). The habitat has  $T_1$  good and  $T_0$  poor territories. If  $n_{M1} + n_{M0} > T_1 + T_0$ , and if many males survive migration, it is possible that some males cannot breed at all; analogously for females ( $n_{F1} + n_{F0} > T_1 + T_0$ ).

Individuals know their own quality, and can make migration decisions accordingly. The 'decision' is modelled as the target arrival date,  $t$ , which is given independent values for each of the four classes of individuals, using individual category as a subscript (e.g.  $t_{M1}$ ). On each day of a migration season that lasts from  $d = 0$  to  $d = D$ , non-arrived birds move to one of the 'arrived' states (Appendix I) according to the geometric probability distribution  $P(d, p)$  (Fig. 1). For example,



**Fig. 1.** Arrival date distributions in the two models. In model 1, arrival dates follow a geometric distribution, illustrated for target dates  $t = 5$  (open dots) and  $t = 10$  (filled dots). In model 2, birds can control their arrival probabilities fairly accurately, exemplified for target date  $t = 10$  (line histogram). An average bird arrives on day 10·32 in this case.

the number of high-quality males that arrive on day  $d$  is  $P(d, p_{M1}) n_{M1}$ . The interpretation of the geometric distribution is that significant numbers of birds arrive as soon as the migration season begins, but the exact fraction arriving on day 0, as well as the length of the ‘tail’ of later-arriving birds, depends on the target arrival date. The above definition makes the average arrival date equal to the target date,  $t$ .

After having arrived, the bird may undergo several changes in state. The state changes are detailed in Appendix II; here we give a verbal description. On each day, deaths occur among arrived birds. Corresponding to the biologically realistic assumption that environmental conditions improve as spring progresses, we assume that the daily mortality risk follows a declining function  $\alpha \exp(-\beta t)$ , where  $0 < \alpha < 1$  and  $\beta > 0$ . Parameter  $\alpha$  indicates mortality on day 0, and parameter  $\beta$  the speed of the decrease of daily mortality from its value at day 0. Following Kokko (1999), these two parameters can take different values for birds of different quality such that high-quality birds suffer less from adverse conditions early in the season (thus they are expected to have lower  $\alpha$  and higher  $\beta$  than low-quality birds). Surviving males who do not yet have a territory may then obtain one, but it may take some time before territories are found and ownership is settled; only after this period is it possible for a male to acquire a female. The rate of settling,  $g$ , differs between high- ( $g_1$ ) and low-quality males ( $g_0$ ).

Similar to settling in a territory, pair formation is assumed to take time: for a given number of settled males and arrived females, the number of pairings is proportional to the parameter  $0 < \gamma < 1$  (as a borderline case we may set  $\gamma = 1$ , which assumes minimal delay: all available individuals mate on their first day if opposite-sex individuals are available). Within each day pairings occur in an ordered fashion, which reflects mate choice: males residing on good territories are mated first; within a territory, quality class males of high individual quality are mated first, and within each territory-male combination, females of high quality are allowed to pair first. The exact number of pairs that follows from these assumptions is given in step 4 of Appendix II. This

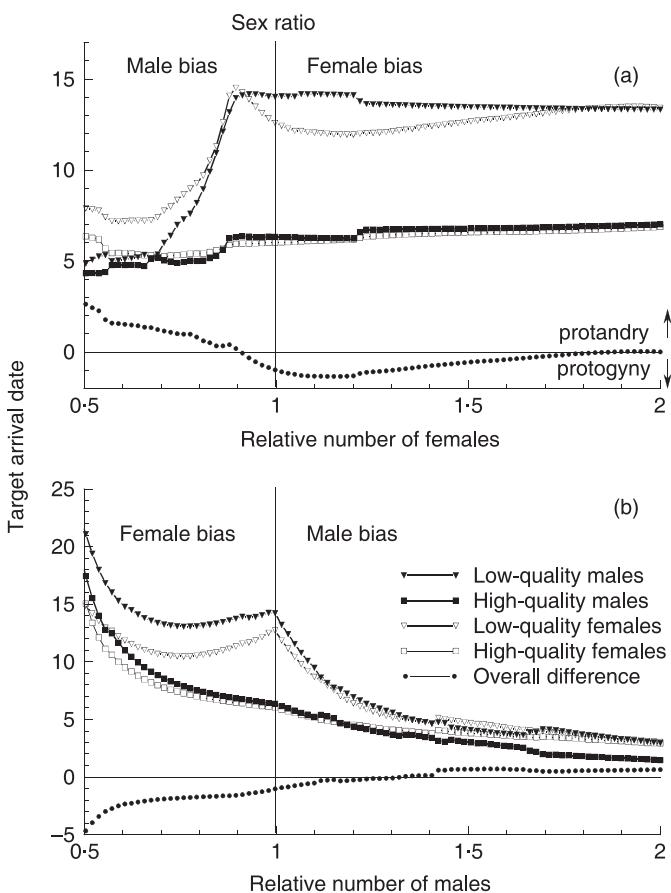
order of events reflects our assumption that females base their choice primarily on good quality habitat, but that they also pay attention to mate quality, and that high-quality females have priority access to territories and mates. The process is repeated for each day of the arrival season, after which the fate of birds is known and fitness can be assigned: the model tracks how many birds are alive and paired, and the quality of the territory and mate. Having a high-quality mate and/or a good territory by the end of the migratory season both independently improve fitness (for a full list of fitness values see Appendix I). Expected fitness is the weighted mean of fitness of individuals in each state. The weights are the state-specific numbers of individuals at the end of the arrival season, which simultaneously indicates the probability that a single individual ends up in the focal state. Individuals who died obviously have zero fitness in the calculation.

Settling, pairing and deaths are modelled as fractions of individuals changing state, which means that the model incorporates biologically realistic stochasticity: despite her priority access, a high-quality female sometimes mates later than a low-quality female. We are able to calculate exact fitness consequences as the arrival date distribution and the expected fates of individuals can be computed precisely, and we always found a single stable equilibrium for target arrival dates  $t_{M1}$ ,  $t_{M0}$ ,  $t_{F1}$  and  $t_{F0}$ .

A typical model outcome shows the importance of the adult sex ratio (Fig. 2). In Fig. 2a, 100 males compete for 100 territories, while the number of females varies from 50 (relative number of females  $x = 0.5$ , Fig. 2a) to 200 ( $x = 2$ ). Male-biased sex ratios in Fig. 2a yield a positive difference between female and male arrival dates, i.e. protandry. High-quality males arrive first, followed by either high-quality females or low-quality males, depending on the exact value of  $x$ . With more than 0·9 females per male, the patterns are reversed: within each quality class, females arrive before males. Conclusions remain similar when male rather than female numbers are varied (Fig. 2b): male-biased sex ratios lead to protandry, although once again the switchpoint is not exactly at a 1 : 1 sex ratio.

Thus, the more numerous sex has to compete for breeding opportunities more intensely, and arrives earlier. In this respect, Fig. 2 could be seen to simply describe the conditions for sex-role reversal in arrival times (Reynolds *et al.* 1986). However, we built into the model an assumption of sexual asymmetry: males gain territories first, and females settle only in territories that are already defended by a male. Therefore, the model is not a simple symmetrical description of sex roles. Instead, it examines how an assumed asymmetry in sex roles concerning breeding site acquisition is reflected in sex-specific arrival times. If the rank advantage argument explains protandry, our model should predict that overall males arrive earlier, unless other factors such as a strongly female-biased sex ratio interfere.

Figure 2 provides little evidence that the rank advantage hypothesis *per se* promotes early male arrival beyond



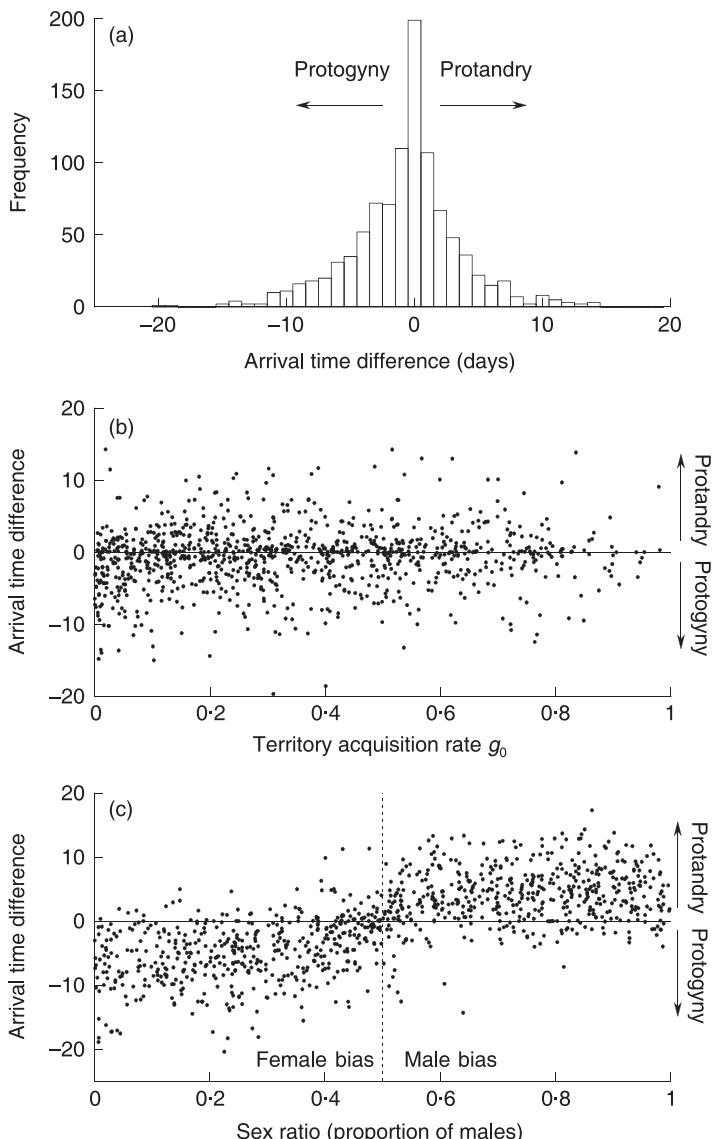
**Fig. 2.** Target arrival dates  $t$  in the numerical analysis (model 1) vary according to the numbers of individuals competing for territories. Low dates indicate early arrival, and ‘overall difference’ is the mean of arrival dates of all females minus that of males, thus positive values indicate protandry and negative values protogyny. The number of territories is  $T_1 = 30$  and  $T_0 = 80$ . In (a), the number of males is  $n_{M1} = 40$ ,  $n_{M0} = 60$ , and the number of females is  $n_{F1} = 40x$  and  $n_{F0} = 60x$ , where the relative number of females is given on the  $x$  axis. Unity thus means that there are as many females of each quality as there are males, and values  $x > 1$  indicate a surplus of females such that the ratio of high to low-quality females remains constant. In (b), the number of females is  $n_{F1} = 40$ ,  $n_{F0} = 60$ , and the number of males varies as  $n_{M1} = 40x$  and  $n_{M0} = 60x$ . Other parameters:  $\alpha = 0.7$ ,  $\beta = 0.4$  (for low-quality individuals);  $\alpha = 0.8$ ,  $\beta = 0.3$  (for high-quality individuals);  $g_1 = 0.9$ ,  $g_0 = 0.5$ ,  $\gamma = 0.5$ ,  $w_T = 1$ ,  $w_M = w_F = 0.1$ ,  $d = 50$ .

that of females. First, even though we assumed that males need time to settle in territories, the zones of protandry (positive value of ‘overall difference’, Fig. 2) are not larger than those of protogyny. Secondly, the rank advantage hypothesis should operate at its purest at sex ratios of unity: as soon as there is a sex ratio bias, the mate opportunity hypothesis interferes as one of the sexes experiences limited access to mates. However, unbiased sex ratios predict protogyny (Fig. 2), females arriving on average 1 day before males.

Figure 2 uses particular parameter values, and one could hypothesize that if settling on territories and/or mate acquisition take longer than assumed in Fig. 2, the rank advantage hypothesis could become stronger. To avoid presenting a narrow focus of particular parameter combinations only, we ran the model at unity sex ratio (100 males, 100 females competing for 100 territories of variable quality), using a set of 1000 randomly and independently chosen parameter combinations in the biologically feasible range. All the following were chosen as independently and uniformly distributed random numbers (range in brackets): the proportion of males

that are high quality (0 ... 1), the proportion of females that are high quality (0 ... 1), the proportion of good territories (0 ... 1, the total number of territories being 100), length of the arrival season  $D$  (20 ... 60), pairing speed  $\gamma$  (0 ... 1) and the fitness benefits  $w_T$ ,  $w_F$  and  $w_M$  (1 ... 5, 0 ... 0.2 and 0 ... 0.2, respectively). Mortality parameters  $\alpha$  and  $\beta$  were drawn independently twice (0 ... 1), with the larger value of  $\alpha$  and the smaller of  $\beta$  chosen to represent poor quality individuals; similarly for the rate of settling on territories  $g$  (range 0 ... 1, lower of the two values chosen to represent low-quality individuals).

Randomized trials with unbiased sex ratios failed to produce protandry more often than protogyny (Fig. 3a), and yielded no support for the idea that longer periods of settling or pair formation favour protandry. If anything, faster settling of low-quality males shows a statistical relationship with protandry, but this effect is too weak for any degree of biological significance (Fig. 3b). Repeating this procedure with varying sex ratios, however, shows that adult sex ratio performs well when predicting protandry or protogyny (Fig. 3c). The exceptions (i.e. the anomalous solutions in the top-left or bottom-right of Fig. 3c) do



**Fig. 3.** Differences in male and female arrival times based on 1000 randomized trials. In (a, b), there are 100 males and 100 females. (a) Protandry calculated as the difference (females – males) between mean target dates of the two sexes, negative values (53·4% of cases) indicating protogyny. Mean of distribution =  $-0\cdot70 \pm 0\cdot13$ . (b) Protandry is very weakly, although statistically significantly, associated with fast territory settlement rates in low-quality males ( $r = 0\cdot101$ ,  $P = 0\cdot0013$ ). Settling rates of other males, or mate acquisition rates, show no relationship at all ( $P > 0\cdot4$ , not shown). (c) Randomization performed as in (a, b), but additionally the sex ratio (proportion of males) follows a uniform distribution between 0 and 1, while the total number of individuals is kept constant at 200. Lines divide the graph into regions in which sex ratio alone correctly predicts protogyny (bottom left) or protandry (top right).

not have territory settling or pairing rates that differ from the distribution from which they are drawn ( $P > 0\cdot05$  in  $t$ -tests testing against an exactly known mean). Instead, exceptions occur when high- and low-quality individuals are very different in terms of territory settling rate  $g$  or mortality patterns  $\alpha$  and  $\beta$ , if the sex ratio differs little from 0·5, if the arrival season is short, or the fitness effects of being paired to a high-quality bird are small ( $P < 0\cdot05$  in each case; however, multiple variables were tested in Fig. 3, and the last two variables are not significant if a Bonferroni correction is applied). These exceptions shift protogyny to protandry or vice versa approximately equally often, thus the rank advantage hypothesis produces no consistent bias towards protandry.

Trials with distributions other than a geometric distribution for the arrival date did not change this conclusion (not shown).

#### MODEL 2. INDIVIDUAL-BASED SIMULATION WITH EXTRA-PAIR PATERNITY

Models that assume that males can mate with multiple females often produce protandry (Bulmer 1983; Iwasa *et al.* 1983). In socially monogamous birds, multiple mating means sperm competition and extra-pair paternity. We built an individual-based simulation that allows sperm competition to take place, which also allows us to examine possible limitations of the numerical approach above.

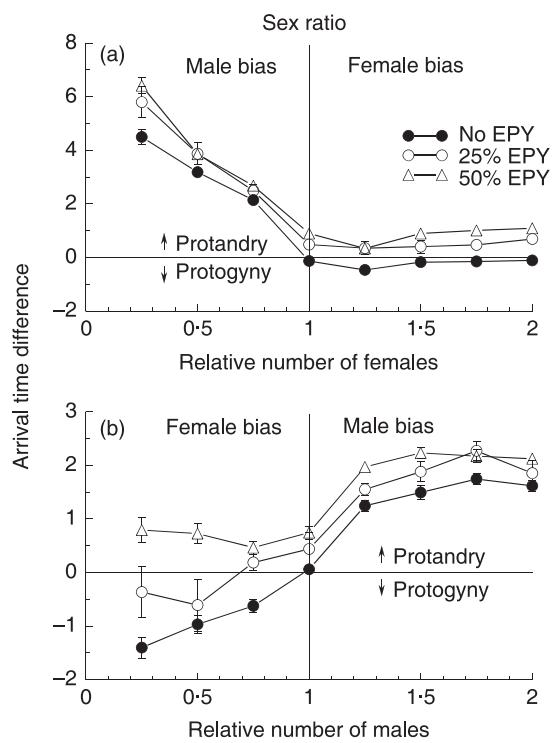
We assume a population that consists of a variable number of males and females. The probability of arriving on day  $d$ , conditional on not having arrived yet, equals  $P(d, t) = \{1 + \exp[-2(d-t)]\}^{-1}$ . The constant 2 in the expression specifies the shape of the arrival curve, and is chosen such that birds are given the ability to control their arrival date much more precisely than in the previous numerical analysis (Fig. 1). Each individual possesses two loci controlling their target arrival date  $t$ . One,  $a$ , is expressed in males only and specifies the male's target arrival date (see Fig. 1 for the relationship to the actual date), the other,  $b$ , is the target date expressed in females. Both loci can take any allelic value between 0, the start and  $D$ , the end of the migration season. The conditional probabilities imply that the mean arrival date in the second model is close to, but not exactly equal to, the target date; we report mean arrival dates as these correspond to what can be observed in nature.

The details of the arrival process are given in Appendix III; the main assumptions are summarized here. We assume a constant number ( $T$ ) of breeding sites, that vary in quality from 1 to  $Q_{\max}$  (where  $Q_{\max}$  is an integer  $\geq 1$ ) as an integer-valued uniform random distribution, i.e. the probability of each value is  $1/Q_{\max}$ . As in model 1, we assume that daily mortality on breeding grounds declines exponentially with time  $t$ , the rate of decline given by a parameter  $\beta$  (step 4 in Appendix III). For simplicity, we ignore quality differences between individuals and do not include variation in mortality on day 0 (i.e. model 2 includes no  $\alpha$ ). Biases in the adult sex ratio are introduced by setting upper ceilings for the numbers of females and males that can exist in the population (step 10 in Appendix 3).

Arrived females choose mates among males who have a territory but not yet a social mate. The proportion of extra-pair young is  $p_E$ , such that each offspring produced by the female is an extra-pair young (EPY) with probability  $p_E$ . The extra-pair sire is chosen randomly among the males who have arrived, and are alive, at the time the female arrives on the breeding grounds. The offspring have mutations in the loci that determine migratory behaviour with a low probability  $\mu$ .

For visual clarity, the simulation results are depicted as the average arrival time difference between females and males, given as the average genotypic value of  $a$  minus the average genotypic value of  $b$  after a minimum of 100 years of simulation in 50 independent replicates. Note that although the target arrival date does not strictly equal the mean of the arrival date distribution, the differences between two target dates equal the average differences between two observed dates. The arrival time difference is positive if males arrive first (protandry), and negative values indicate protogyny. To ensure that distributions had stabilized, simulations were run until the correlation coefficient of the arrival time difference against time (generations) was in the range  $0 \pm 0.005$ ; however, simulations were always run for at least 100 generations.

When there is no extra-pair paternity, the results (Fig. 4) are in line with the numerical approach (Fig. 2). Unbiased

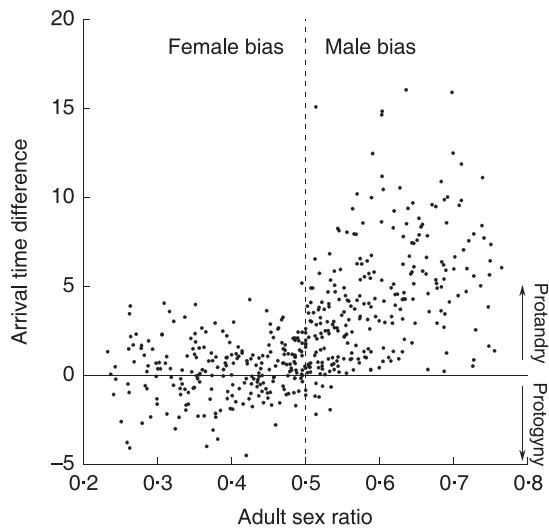


**Fig. 4.** The results of the simulation model of differences in male and female arrival times. Each data point is based on 50 simulation runs. Means  $\pm$  SE are given, although the latter are often too narrow to be visible. The percentage of extra-pair young ( $p_E$ ) is 0%, 25% or 50% as indicated by filled dots, open dots and triangles. In (a), there are  $N_M = 200$  males, and female numbers vary from 50 to 400 as given on the x axis. Unity indicates even sex ratios ( $N_M = N_F = 200$ ), and there is no significant difference in arrival times without extra-pair paternity. In (b), there are  $N_F = 200$  females, and male numbers  $N_M$  vary as indicated on the x axis. Again, the sex in excess arrives first. Other parameters:  $\beta = 0.4$ ,  $\mu = 0.01$ ,  $D = 40$ ,  $T = 200$ .

sex ratios yield no significant protandry or protogyny (Fig. 4a: protandry  $= -0.13 \pm 0.10$ , Student's  $t = -1.31$ ,  $P = 0.20$ ; Fig. 4b: protandry  $= 0.06 \pm 0.07$ ,  $t = 0.87$ ,  $P = 0.39$ ). Male-biased sex ratios lead to protandry, and female-biased ratios lead to protogyny (Fig. 4, filled dots). Pronounced protogyny is only found in Fig. 4b, where males are in short supply in such a way that the total number of males falls below that of territories. In the rightmost points in Fig. 4a males are similarly in short supply, but now the number of males equals that of territories. Both sexes are thus limited by the availability of good habitat, and are selected to arrive almost equally early.

Increasing the proportion of EPY always shifts the solutions towards protandry (Fig. 4). However, very high proportions of EPYs are required to overturn the effects of adult sex ratio. At 25% EPY there is a discernible effect on protandry, but one that makes little qualitative difference. Fifty per cent EPY yields protandry regardless of adult sex ratios.

Trials with different choices for parameters  $\beta$ ,  $\mu$ ,  $Q_{\max}$  and  $T$  yielded similar results. To reach an overview of



**Fig. 5.** Simulation of differences in male and female arrival times based on 500 randomized trials, plotted against adult sex ratio  $N_M/(N_F + N_M)$ . The scatter reflects variation in other parameters. Because the proportion of extra-pair young is distributed between 0 and 0.5, there are more solutions with protandry ( $n = 383$ ) than protogyny ( $n = 105$ ). In the 12 remaining trials low  $\beta$  caused such high mortality that the population went extinct.

the effects of these parameters, we investigated their joint effect in a randomized trial similar to that used in model 1. We ran single simulation runs with a set of 500 choices for the rate of mortality decline over time,  $\beta$  (uniform distribution with range 0 ... 1), mutation probability  $\mu$  (0 ... 0.2), number of males  $N_M$  (0 ... 0.5), number of females  $N_F$  (50 ... 200), proportion of EPY  $p_E$  (100 ... 200), number of territories  $T$  (50 ... 200) and the variation in territory quality  $Q_{\max}$  (1 ... 10, integer values only). Consistent with Fig. 4, the degree of protandry increased significantly with male numbers  $N_M$  ( $r = 0.25$ ,  $P < 0.001$ ), proportion of EPY  $p_E$  ( $r = 0.11$ ,  $P = 0.018$ ), and decreased with female numbers  $N_F$  ( $r = -0.55$ ,  $P < 0.001$ ) and with available variation in territory quality  $Q_{\max}$  ( $r = -0.19$ ,  $P < 0.001$ ). The effect of other parameters remained non-significant. Protandry remained linked strongly to adult sex ratio but was overall more common than protogyny, as the randomized trials included sperm competition with an average proportion 25% of EPY (Fig. 5).

## Discussion

Our two different modelling techniques help to disentangle the effects of the rank advantage hypothesis and the mate opportunity hypothesis on arrival times in migratory birds. The rank advantage hypothesis is built into both models, as we assume that early arriving birds acquire, on average, better territories. Elements of the mate opportunity hypothesis were included in the form of sperm competition (extra-pair opportunities in the simulation model) and sex ratio biases (both models). Mate acquisition chances did not differ between the sexes

when extra-pair paternity is excluded (first model: always, second model: when EPY = 0) and adult sex ratios were set to unity, therefore under these assumptions the rank advantage hypothesis operates alone.

Our most intriguing conclusion is that the rank advantage hypothesis *per se* fails as an explanation of protandry in birds. The hypothesis states that ‘competition for territories selects for the earliest arriving males’ (Morley & Ydenberg 2001); however, our models do not predict protandry in the absence of mating opportunity differences (unity sex ratio and no EPY). Morley & Ydenberg (2001) cite Kokko (1999) for the argument that competition advances male arrival dates, yet an examination of the model in Kokko (1999) reveals that it is not restricted to considering males only: instead, it only specifies competition within a single sex. If there are two sexes, both of which are interested in securing a good breeding location, both should be expected to advance their arrival to a point that is, finally, counter-selected by increasing costs of early arrival.

What about the argument that females do not benefit from arriving earlier than males as they cannot secure a breeding position before males have arrived? Our models assume that males have to settle first, before they can acquire females on their territories. Both settling and mate acquisition take time, yet the protandry-promoting effect is negligible. Individuals should arrive particularly early if they are competing for a resource that is in short supply (Kokko 1999). Therefore, if both sexes suffer equally high costs when arriving early, the sex that competes for a scarcer resource should arrive first. Early arriving males are competing for a resource that is widely available (territories so far vacant), while early arriving females compete for territories that already have a male. The latter is a resource that is scarce at least initially, when settling has not yet taken place, and potentially later too, when a continuous supply of new males is continuously ‘used up’ by arriving females.

Therefore females aiming to pair with the best males in best territories should, theoretically, arrive early to wait for this chance to happen. This counteracts the argument that females can simply wait until males have settled. Human societies offer a good analogy: if very attractive seaside apartments are being built, one should not relax and wait because building will take time. Instead, ownership should be secured during or even before the building process starts, if the seafront is a hotly contested resource. Of course, there are also situations in which males who have settled are not in short supply, but this requires male-biased sex ratios (Fig. 3c).

As protandry appears to be the norm in bird populations (e.g. Gunnarsson *et al.* 2004, 2006; Smith & Moore 2005), one must explain why we do not see females that arrive early and then wait for males to occupy territories for them. The first possible explanation is that if females really did arrive that early, they would also be selected to do the defending of territories themselves, thus our assumption that they have to wait for males becomes incorrect. The case would then correspond to

proper sex-role reversal, and protogyny is indeed observed in these cases (Oring, Reed & Maxson 1994), although not always associated with territoriality (Reynolds *et al.* 1986). This solution applies to special cases of sex-role reversal. As a general explanation we favour another possibility: the rank advantage hypothesis alone does not predict observed patterns of protandry, and it has to be spiced up with some aspects of the mate opportunity hypothesis before theory consistently predicts protandrous arrival times.

Our models consider mating opportunities in two distinct, but not mutually exclusive ways: by varying adult sex ratios and (in the simulation model) by including extra-pair paternity. Both our models predict that sex ratio biases have a very strong effect on arrival times. Significantly male-biased sex ratios consistently produce protandry and female-biased ratios produce protogyny (except if the effects of extra-pair paternity are strong; see below). This suggests that protandry in birds is mainly a result of sexual selection for mating opportunities in males, and it is therefore a very similar phenomenon to protandry in other well-studied taxa, such as arthropods, for which the mate opportunity hypothesis is considered widely to be appropriate (reviewed in Morbey & Ydenberg 2001).

What is the evidence for sexual selection being responsible for protandry? For sex ratios to drive the prevalence of protandry in birds, adult sex ratios should be consistently male-biased. In birds, there is indeed evidence that adult mortality appears to be significantly female-biased (Promislow, Montgomerie & Marten 1992; Liker & Székely 2005). This is an unusual pattern compared to mammals, for example, in which sexual selection acting on males increases male mortality beyond that of females (Promislow 1992; Moore & Wilson 2002). Various hypotheses for female-biased mortality in bird species have been proposed, including mortality costs associated with female-biased parental care (Owens & Bennett 1994), lower levels of sexual competition in birds than mammals and higher mortality risks for the heterogametic sex (females in birds and males in mammals) through the effects of deleterious recessive mutations (Liker & Székely 2005). Because we predict minor biases in the adult sex ratio to be sufficient to drive protandry, female-biased mortality could easily cause protandry.

Sperm competition (extra-pair paternity) provides another potential form of the mate opportunity hypothesis. We found that extra-pair paternity helps to explain protandry, but the effect is milder than that of biased sex ratios. 25% EPY produces a slight shift towards protandry, and very high extra-pair paternity (50%) is required before protandry persists under female-biased sex ratios. In a survey of extra-pair paternity, Griffith, Owens & Thuman (2002) found that only 3% (four of 129) of bird studies reported 50% or more EPY. The median proportion of EPY in this data set (which includes many nonmigratory species) was only 5.2%. Therefore, extra-pair paternity can help to shift arrival patterns towards stronger or more widespread protandry,

but it appears likely that male-biased sex ratios perform better as a general explanation for the near ubiquity of protandry in migratory birds.

Our model assumed that females do not accept any males as extra-pair sires who arrived later than the female, even if the actual copulation happened later. This assumption will lead to a slight exaggeration of the benefit of protandry, if females in reality sometimes mate with extra-pair males much later in the season (as it is then possible for a male to mate even if he has arrived late). The protandry-enhancing effect of extra-pair paternity is an overestimate if this assumption does not hold. However, Birkhead & Möller (1998) pointed out that early arriving males may indeed have more opportunities for multiple mating as levels of competition at the start of the season will be low, as few males have arrived, and as early clutch completion may allow early males to spend relatively less time mate-guarding when late females arrive.

Empirical support for the mate opportunity hypothesis is reported in Rubolini, Spina & Saino (2004): protandry across 21 trans-Saharan migrant bird species is positively correlated with sexual dichromatism, an indicator of sperm competition. Rubolini *et al.* (2004) found no evidence of a correlation between sexual size dimorphism and protandry, which would have provided support for the rank advantage hypothesis, because male–male competition for territories should result in selection for larger size in early arriving males. Extra-pair paternity has also been found to positively influence protandry in a comparison of five migratory species (Coppack, Tottrup & Spottiswoode 2006), providing additional correlational support for the mate opportunity hypothesis. Thus, empirical studies and our theoretical approach both emphasize the importance of sexual selection in driving protandry.

While our study confirms the prediction that, all other things being equal, stronger sperm competition should lead to greater protandry (Rubolini *et al.* 2004; Coppack *et al.* 2006), we also predict that sex ratio biases and the consequent sexual selection on males should be an even stronger determinant of protandry. The mate opportunity hypothesis follows slightly different rules in socially monogamous birds than the same hypothesis in, for instance, arthropods. In migrant birds with social monogamy, multiple mating is more constrained than in simpler mating systems. The majority of young are usually the result of within-pair copulations, and these do not contribute to siring opportunities for all males in the population. This explains why adult sex ratios can be the stronger determinant of arrival patterns for birds: this ratio determines whether all males can gain a (social) mate or not. If they cannot, females immediately become a rare resource, and strong protandry is predicted whether or not males can achieve multiple matings. Future empirical tests of the ideas presented here will therefore primarily require information on sex ratios of migratory birds. Unfortunately, measuring sex ratios in migrants is a difficult task, given the very large

spatial scales involved and complications such as sex-biases in distribution, habitat use and visibility. However, if sex ratios can be measured, ideally in sufficient species to allow comparative analyses, our models provide a series of clear predictions:

1. Greater protandry when sex ratios are more male-biased.
2. Less clear protandry when both sexes suffer from a shortage of (good) breeding locations.
3. Consistent with earlier ideas (Reynolds *et al.* 1986), protogyny should occur when sex ratios are female-biased, although in cases where polyandry combines with polygyny, the multiple mating opportunities for males can select for protandry once again.
4. All other factors being equal, a greater proportion of EPY – or other forms of multiple mating – should select for greater protandry, but significant variation in adult sex ratios should override this effect.

To conclude, we echo Morbey & Ydenberg's (2001) call for more theoretical and empirical work that aims to disentangle different selective pressures acting on male and female arrival patterns. Although the rank advantage hypothesis has been considered widely as the principal force driving protandry in migratory birds, this may reflect a focus on the selective pressures operating on a single sex only. Once one considers that outcompeting same-sex individuals is advantageous for members of either sex, a sexual asymmetry in mate acquisition prospects is required to explain protandry. The rank order of arrival remains important, but this is primarily because it determines the probability of finding a mate (or mates), which is difficult if one happens to be a member of the majority sex.

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## Appendix I

Possible individual states and fitness (in brackets) of arrived birds at the end of the migration season. We set a baseline fitness  $w = 1$  for the members of a low-quality pair on a poor territory. Fitness improves by  $w_T$  if the territory is good, by  $w_M$  if the male of the pair is high quality, and by  $w_F$  if the female of the pair is high quality.

### MALE STATES

1. Low-quality individual, not arrived.
2. High-quality individual, not arrived.
3. Low-quality individual, arrived, no territory (0).
4. High-quality individual, arrived, no territory (0).
5. Low-quality individual, arrived, has good territory (0).
6. High-quality individual, arrived, has good territory (0).
7. Low-quality individual, arrived, has poor territory (0).
8. High-quality individual, arrived, has poor territory (0).
9. Low-quality individual, arrived, has good territory and high-quality female ( $1 + w_T + w_F$ ).
10. High-quality individual, arrived, has good territory and high-quality female ( $1 + w_T + w_M + w_F$ ).
11. Low-quality individual, arrived, has good territory and low-quality female ( $1 + w_T$ ).
12. High-quality individual, arrived, has good territory and low-quality female ( $1 + w_T + w_M$ ).
13. Low-quality individual, arrived, has poor territory and high-quality female ( $1 + w_F$ ).
14. High-quality individual, arrived, has poor territory and high-quality female ( $1 + w_M + w_F$ ).
15. Low-quality individual, arrived, has poor territory and low-quality female (1).
16. High-quality individual, arrived, has poor territory and low-quality female ( $1 + w_M$ ).

### FEMALE STATES

1. Low-quality individual, not arrived.
2. High-quality individual, not arrived.
3. Low-quality individual, arrived, no territory (0).
4. High-quality individual, arrived, no territory (0).
5. Low-quality individual, arrived, has good territory and high-quality male ( $1 + w_T + w_M$ ).
6. High-quality individual, arrived, has good territory and high-quality male ( $1 + w_T + w_M + w_F$ ).
7. Low-quality individual, arrived, has good territory and low-quality male ( $1 + w_T$ ).
8. High-quality individual, arrived, has good territory and low-quality male ( $1 + w_T + w_F$ ).
9. Low-quality individual, arrived, has poor territory and high-quality male ( $1 + w_M$ ).
10. High-quality individual, arrived, has poor territory and high-quality male ( $1 + w_M + w_F$ ).
11. Low-quality individual, arrived, has poor territory and low-quality male (1).
12. High-quality individual, arrived, has poor territory and low-quality male ( $1 + w_F$ ).

## Appendix II

### DETAILS OF MODEL 1 (NUMERICAL ANALYSIS OF ARRIVAL RATES)

The analysis follows male and female numbers  $M_{i,j}(t)$  and  $F_{i,j}(t)$  through time steps  $d = 0$  to  $D$ . The subscript  $i$  refers to states as indicated in Appendix I, and  $j$  refers to the time step when the bird arrived (not used for birds not yet arrived). Before the onset of migration ( $d = 0$ ), we have  $M_1(0) = n_{M1}$ ,  $M_2(0) = n_{M0}$ ,  $F_1(0) = n_{F1}$ ,  $F_2(0) = n_{F0}$  and  $M_{i,j}(0) = F_{i,j}(0) = 0$  for all other states  $i$  and  $j$ . Each day ( $d$ ) of the migratory period, the following steps are computed to keep track of the dynamics of arrival and territory acquisition:

1. Arrival: the number of males in state  $i = 1$  (low quality, not arrived yet) diminishes by  $n_{M0} P(d, p_i)$ , where  $d$  is the current day,  $P(d, p_i) = p_i (1 - p_i)^d / \sum_{i=0}^D p_i (1 - p_i)^d$ , and  $p_i$  is solved from  $\sum_{d=0}^D dP(d, p_i) = t_{M0}$ . Here,  $p_i$  ( $0 < p_i < 1$ ) is a parameter that determines the mean of the distribution, and the value of  $p_i$  that corresponds to a specific target arrival date  $t$  is numerically solved from  $\sum_{d=0}^D dP(d, p) = t$ . The same number is added to males in state  $i = 3, j = t$  (low quality, arrived at time  $t$ , no territory). Similarly for all types of individuals – males and females of either quality – who have not arrived yet.
2. Death: early arrival imposes mortality risks. Numbers of individuals of all states with  $i \geq 3$  diminish by a factor  $\alpha \exp(-\beta d)$ .  $\alpha$  and  $\beta$  are quality-specific parameters. Numbers of females in states 3 onwards are adjusted: females move to states 3 and 4 if their social mate died. The number of vacant territories is accordingly increased.
3. A fraction  $g_1$  of high-quality males and a fraction  $g_0$  of low-quality males with no territory (states  $i = 3, 4$ ) acquire a good territory; however, the fractions are adjusted to sum up to the number of vacant good territories if the result indicates more acquisitions than there are vacant good territories. The number of vacant good territories diminishes according to the number of acquisitions. The process is repeated for poor-quality territories if such are available (the order reflects a preference for good over poor breeding sites in all males, and also superior competitive ability of high-quality males if  $g_1 > g_0$ ).
4. Pairings occur among arrived and single individuals, controlled by the parameter  $\gamma$ . These occur in the following order, indicating the quality combination ‘territory–male–female’: good–high–high; good–high–low; good–low–high; good–low–low; poor–high–high; poor–high–low; poor–low–high; poor–low–low. This order reflects the assumption that high-quality females are superior competitors and have priority access to their preferred options, and that females pay more attention to territory than to male quality: their first option is to go for a good territory occupied by a high-quality male, then for a good territory occupied by a low-quality male, followed by a poor territory occupied by a high-quality male, and finally a poor territory owned by a low-quality male. In each case, the number of pairings is the smallest alternative of the following three numbers:

$\{\gamma \sum_j M_{i,j}(d) \sum_j F_{i,j}(d), \sum_j M_{i,j}(d), \sum_j F_{i,j}(d)\}$ , which ensures that there cannot be more pairings than available members of each sex. Numbers  $M_{i,j}(d)$  and  $F_{i,j}(d)$  are adjusted accordingly (e.g. poor–high–low pairings shift female numbers from  $i = 3$  to  $i = 9$  and males from  $i = 4$  to  $i = 16$ ).

Once all the time steps are computed, the expected fitness of a bird that arrives on day  $j$  is computed as the weighted sum  $W_{Mj} = \sum_{i=9}^{16} M_{i,j}(D) w_{Mi}/n_{Mi}$  for males and  $W_{Fj} = \sum_{i=5}^{12} F_i(D) w_{Fi}/n_{Fi}$  for females. Summing from  $i = 5$  (females) or  $i = 9$  (males) onwards, and counting fitness at  $d = D$ , together ensure that fitness is zero if the individual does not survive the arrival, or fails to secure a territory and a mate. For fitness values see Appendix I.

Selection to shift arrival rates is established, if an alternative arrival schedule leads to improved fitness. This was evaluated numerically, choosing a small deviation ( $\delta = 0.001$ ) for each value of target date  $t$  and evaluating the sign of  $\sum_{d=0}^D P(d, p_{t-\delta}) W_{Mi} - \sum_{d=0}^D P(d, p_{t+\delta}) W_{Mi}$ . Positive (negative) values indicate selection for earlier (later) arrival. The population strategy was shifted in the direction of selection, until no further change was found. We always found the same equilibrium regardless of starting values of  $t_{M1}, t_{M0}, t_{F1}$  and  $t_{F0}$ .

### Appendix III

#### SIMULATION DETAILS (MODEL 2)

The population is initiated with  $N_M$  males and  $N_F$  females, and  $T$  territories with randomly distributed qualities (uniform distribution of integers between 1 and  $Q_{\max}$ ). Each individual has allelic values  $a$  and  $b$  which are randomly chosen real numbers, distributed uniformly between 0 and 40. Each generation, the following steps are computed:

1. Start with  $t = 0$ .
2. Each individual who has not yet arrived, arrives if a random number, uniformly distributed between 0 and 1, falls below the threshold  $P(d, a) = \{1 + \exp[-2(d - a)]\}^{-1}$  (if the individual is a male) or  $P(d, b) = \{1 + \exp[-2(d - b)]\}^{-1}$  (if female).

3. Each female who has arrived but has not yet chosen an EPC partner does so among the so-far-arrived males.

4. Each individual who has arrived dies with probability  $e^{-\beta t}$ . As in model 1, females become homeless if they already had a mate and their mate dies.

5. Arrived males without a territory are assigned to territories; males choose the best territories currently available. The order in which individuals are allowed to choose is random among arrived males. Some males may be left without a territory if no vacancies are available.

6. Arrived females without a territory are assigned to territories, if unpaired territorial males are available. Females choose the best territories currently available. The order in which individuals are allowed to choose is random.

7. If  $d < 40$ , increase  $d$  by one time unit, and repeat from step 2 onwards.

8. Breeding commences. Females who are on a territory produce offspring. The total number of offspring equals the quality of the territory. Offspring sex is randomly determined for each offspring independently (1 : 1 primary sex ratio). Each offspring's paternity is similarly independently determined: the probability that the sire is the extra-pair male is  $p_E$ , and with probability  $1 - p_E$  the sire is the social mate of the female. Offspring inherit each allelic value randomly from either parent.

9. With a small probability  $\mu$ , any allelic value  $a$  or  $b$  in an offspring mutates to a different uniformly distributed random value between 0 and 40.

10. Autumn migration commences, vacating all territories. The winter population consists of parents and offspring of the previous summer. If there are more than  $N_F$  females, a random subset is removed so that  $N_F$  are left; similarly for males (ceiling  $N_M$ ).

This procedure is repeated until the difference between female and male target arrival times stabilizes, i.e. the correlation coefficient between the difference and time falls between  $-0.005$  and  $+0.005$ . To avoid stopping at accidental low correlation values during transient dynamics, at least 100 generations were always run.