

Competition for early arrival in migratory birds

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Summary

1. It is widely accepted that the arrival order of migratory birds is correlated with the condition of the birds, which leads to high quality individuals occupying prime sites. However, the theoretical backgrounds for this argument have been lacking. A simple game-theoretic model of arrival timing is provided which investigates the evolutionary stability of condition-dependent arrival order in territorial migrant birds.

2. Competition for territories or other priority-dependent benefits can lead to arrival dates far preceding the cost-minimizing date (the optimum date in the absence of competition) for all but the weakest individuals. Increasing the number of competitors can generate a ‘cascading’ competition for early arrival, which advances arrival dates further apart from the individual optimum dates for the onset of breeding.

3. At equilibrium, arrival order corresponds strictly to condition order only if marginal costs of advancing arrival are always larger for individuals in lower condition. If spring mortality vacates territories for later-arriving birds, the criterion for ‘honest’ arrival order becomes still stricter: differential survival costs should exist, but survival differences among individuals (or, alternatively, territory quality differences) should not be very large.

4. If the habitat is saturated so that there is a risk of not obtaining a territory at all, or if worst territories are of much lower value than the rest, competition may lead to the majority of the population arriving within a fairly short interval, followed by a much later floating fraction. This synchrony in the arrival of breeders imposes an increasing cost for the lesser fit breeding birds. Thus, arrival costs paid are not necessarily highest for earliest arriving individuals, but for those who have the most to lose if they drop a few steps in the arrival order.

5. Competition for high quality territories can also lead to partial migration, in which case birds in good condition are expected to be most likely to remain resident.

Key-words: floating, partial migration, protandry, seasonal optimization, territory acquisition.

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Introduction

In migratory birds, individuals of higher phenotypic quality are commonly observed to arrive and mate first (Flood 1984; Francis & Cooke 1986; Hill 1988; Møller 1990, 1994a,b; Enstrom 1992; Lundberg & Alatalo 1992; Lozano, Perreault & Lemon 1996). This phenomenon is commonly explained by the

reasoning that early birds gain best territories, but only birds in good condition will be able to survive the costs associated with early arrival. However, it has never been put into the form of a rigorous model: although Møller (1994a) cites Parker & Courtney (1983) in this sense, their model does not refer to a hierarchy of individual qualities but to a hierarchy of resources (food as a resource for females; females as a mating resource for males). Models of protandry exist, deriving evolutionarily stable arrival or emergence date distributions, but these assume equal condition and equal fitness for all individuals (e.g. Wiklund & Fagerström 1977;

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Bulmer 1983a,b; Iwasa *et al.* 1983; Parker & Courtney 1983; Iwasa & Haccou 1994).

In contrast to the assumptions of protandry models, there seem to be real fitness advantages to earlier-arriving or -emerging males. This has been found in insects (Wang, Greenfield & Shelly 1990), for which protandry models have mainly been developed, as well as in birds. In birds, evidence that earlier-breeding birds achieve higher reproductive success is overwhelming (e.g. Daan, Dijkstra & Tinbergen 1990; Verhulst & Tinbergen 1991; Wiggins, Pärt & Gustafsson 1994; Lozano *et al.* 1996; Hasselquist 1998; Verboven & Visser 1998). Because breeding dates are nevertheless not found to evolve towards ever-earlier dates (except at extraordinary events such as climate changes, Crick *et al.* 1997), this points to a role of environmentally determined variance in the condition of birds (Price, Kirkpatrick & Arnold 1988; see also Marra, Hobson & Holmes 1998).

This paper presents a game-theoretic model of evolutionarily stable, condition-dependent arrival dates in territorial birds. The benefit of early arrival is expressed as a priority to a resource such as a superior territory; whether or not this goal is achieved obviously depends on the arrival dates of competitors. The cost, determined by the seasonal environment, is independent of the arrival decisions of others. Results are first developed for a two-player game, which is then extended to an arbitrarily large population. Two different enhancements are also presented, adding different aspects of reality to the model: limited sampling of territories and mortality during spring.

The priority game

Consider two migratory birds competing for two territories. Both the territories and the birds differ in their qualities. Territory values are defined through a fitness benefit B_1 or B_2 gained when settling on them, and bird quality (used synonymously to condition) is defined as the ability to experience low costs by arriving at an early time point t . (For consistency, 'value' refers to the property of the territory, and 'quality' to the property of the bird.) Costs of early arrival decrease with time, but because of individual quality differences, these costs are greater for the low-quality individual at any time, $e_2(t) > e_1(t)$. Delaying arrival for too long is also considered suboptimal (e.g. because of the benefits of early-emerging offspring, Rowe, Ludwig & Schluter 1994; Daan & Tinbergen 1997; Svensson 1997), and this brings about a delay cost $d_i(t)$. The shape of $d_i(t)$ and its relationship to individual condition is irrelevant, as long as it brings about a unique minimum for the total cost $C_i(t) = e_i(t) + d_i(t)$. This minimum reflects the indi-

vidually optimal timing of the onset of breeding (Daan & Tinbergen 1997). By definition, the cost $C_i(t)$ is larger for the inferior individual whenever $t \leq t_i^*$, the point of smallest costs for the superior individual. One may set $C_i(t_i^*) = 0$, i.e. define the cost of any arrival time as the difference to the individual minimum cost (Fig. 1).

It is assumed throughout that territory ownership is determined by priority order. If territory values do not differ ($B_1 = B_2$), both birds should arrive at their respective t_i^* , i.e. the individual cost-minimizing optima. When $B_1 > B_2$, however, both would benefit from being the first one to arrive. There are now two possible equilibria:

1. If the difference in territory value is smaller than the cost of bird 2 arriving at the optimum of bird 1, i.e. $B_1 - B_2 \leq C_2(t_1^*)$, bird 2 has no incentive to try to be first. Hence both birds will arrive at their respective optima t_1^* and t_2^* .

2. If the benefit for bird 2 of obtaining B_1 is high enough, $B_1 - B_2 > C_2(t_1^*)$, the new arrival time T_i will deviate from the cost-minimizing t_i^* for the superior bird 1. The inferior bird now has an incentive to move from $T = t_2^*$ to $T = t_1^* - \epsilon$, i.e. slightly outcompete bird 1. To prevent this, the superior bird has to arrive early enough to render competi-

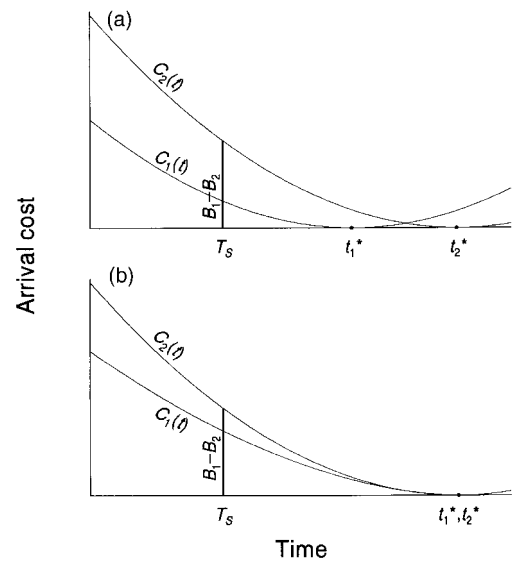


Fig. 1. The arrival game for two birds and two territories. The difference in territory value gives the additional payoff $B_1 - B_2$ for the first-arriving bird. (a) cost functions differ such that the cost-minimizing times t_1^* and t_2^* are different for birds 1 and 2; (b) cost-minimizing time is the same for both individuals. In both cases, the high-quality bird 1 pays a smaller cost than bird 2 for arriving at any time $t < t_1^*$. Because $B_1 - B_2$ is larger than $C_2(t_1^*)$, bird 2 could afford to arrive before bird 1, unless bird 1 counteracts by arriving even earlier. To prevent the incentive of bird 2 to try to acquire the best territory B_1 , bird 1 has to arrive at T_s , where $C_2(T_s) = B_1 - B_2$. Bird 2 will then simply minimize its costs and arrive at t_2^* .

tion not beneficial for the second one, i.e. to the point T_S where $C_2(T_S) = B_1 - B_2$. The subscript 'S' refers to a Stackelberg equilibrium. Stackelberg games (e.g. Rasmusen 1990, p. 79; Osborne & Rubinstein 1994, pp. 97–98) describe situations where 'leaders' choose their actions in order to manipulate the responses of 'followers' to suit the taste of the 'leader'. Here, bird 1, the leader, adjusts its behaviour to make bird 2 (the follower) respond in the best possible way (in the interest of bird 1), i.e. not to try to obtain the best territory. For it to be worthwhile for bird 1 to make this move, its costs $C_1(T_S)$ must remain below the benefits $B_1 - B_2$; but this is always true because $C_1(T_S) < C_2(T_S) = B_1 - B_2$. A similar check guarantees that it does not pay for the inferior bird 2 to become the leader of the Stackelberg game.

Hence there are two possible equilibria: if $B_1 - B_2 \leq C_2(t_1^*)$, both individuals will stay at $T_1^* = t_1^*$ and $T_2^* = t_2^*$, but if the difference in territory values is sufficiently large, $B_1 - B_2 > C_2(t_1^*)$, the first bird will arrive at the Stackelberg date $T_1^* = T_S$ and pay an extra earliness cost $C_1(T_S)$. The second bird then does best by not attempting to obtain the best territory, and will arrive at $T_2^* = t_2^*$. In both cases the early bird is of higher quality.

CASCADING COMPETITION FOR EARLY ARRIVAL

When there are more than two competing birds, all but one individual may have to pay a cost of competition for earliness. Consider a case with three territories, B_1 , B_2 and B_3 , and three birds (Fig. 2a). If bird 1 and 2 were the only competitors, bird 1 would move to point T_S , and bird 2 would remain at t_2^* (the two-bird game described above). However, if $C_3(t_2^*) < B_2 - B_3$, bird 2 is forced to counteract the threat of bird 3 occupying territory B_2 . Bird 2 will move to T_{S2} which satisfies $C_3(T_{S2}) = B_2 - B_3$. At this point, bird 2 may already have moved to a position which is earlier than t_1^* or even the two-bird Stackelberg arrival date T_S for bird 1 (Fig. 2a). Hence, the arrival of bird 2 now threatens the priority of bird 1. As a consequence, bird 1 has to arrive earlier than T_{S2} to counteract it: the new arrival time for bird 1 is T_{S1} which satisfies $C_2(T_{S1}) - C_2(T_{S2}) = B_1 - B_2 \iff C_2(T_{S1}) = B_1 - B_2 + C_2(T_{S2})$. This is a larger requirement compared to the original prevention measure, $C_2(T_S) = B_1 - B_2$. The result is a cascading contest for priority, which leads to both better birds arriving much earlier (T_{S1} and T_{S2}) than they would have done if competing only against each other (T_S and t_2^*) (Fig. 2a).

The 'honest' arrival order of the cascade, where high quality birds arrive before lower quality individuals, only holds true if the marginal costs of mov-

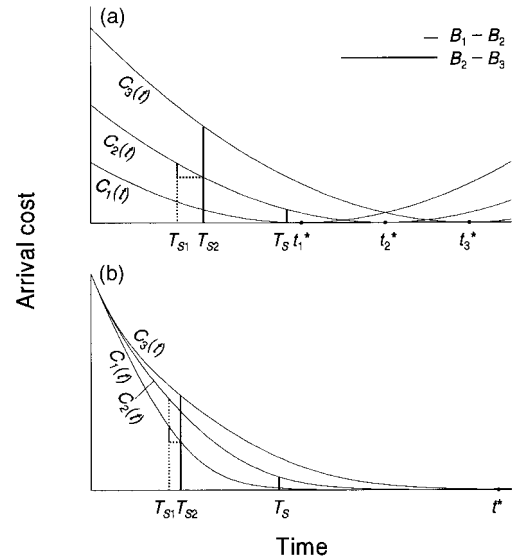


Fig. 2. The cascading competition for early arrival with three birds and three territories. T_S marks the optimum arrival of bird 1 if it competed with bird 2 only. To give a clear example, it is assumed that the third territory is of clearly lower value than the two others: $B_2 - B_3 \gg B_1 - B_2$. (a) Because of the existence of bird 3, bird 2 will move from t_2^* to T_{S2} , to prevent falling to B_3 . But this requires arriving early enough to ensure that bird 2 would arrive earlier than bird 1. Bird 1 has to secure B_1 by moving even further to T_{S1} . Hence at the three-bird equilibrium, birds arrive at T_{S1} , T_{S2} and t_3^* . The two better birds both arrive much earlier than if they had been competing with each other only, in which case their arrival times would have been T_S and t_2^* . Also, bird 2 pays at equilibrium a larger cost than either bird 1 or bird 3: $C_2(T_{S2}) > C_1(T_{S1}) > C_3(t_3^*)$. (b) If the cascade leads to a point where marginal costs of advancing arrival are greater for a lower-quality bird (here, bird 2 at T_{S2}), it does not pay for the superior bird to prevent bird 2 taking over the territory B_1 , because its own costs of doing so would exceed those of bird 2. Instead, bird 2 seeks the point where it pays for bird 1 to stay behind: $C_1(T_{S1}) - C_1(T_{S2}) = B_1 - B_2$. The resulting 'dishonest' arrival order is bird 2 at T_{S1} , bird 1 at T_{S2} , and bird 3 at t_3^* . Without bird 3, the order would have been honest, bird 1 at T_S and bird 2 at t_2^* .

ing to an earlier time point are always higher for low quality individuals (as in Figs 1a,b and 2a). If the superiority of an individual is instead established as a more rapid decrease from an initially equally high cost (as in Fig. 2b), it will not always pay for the superior bird 1 to block bird 2 from acquiring territory B_1 . Instead, if bird 3 forces bird 2 to point T_{S2} where marginal costs are higher for bird 1, bird 2 can now afford to move further left on the time-scale until (at point T_{S1} in Fig. 2b) it prevents its superior competitor from obtaining the best territory! Although bird 1 loses the competition for territory B_1 , it cannot use its cost-free optimum t_1^* either and rely on obtaining at least B_2 , as it would then be threatened by bird 3, as bird 2 was before. The conclusion is then to use $T_1^* = T_{S2}$, $T_2^* = T_{S1}$.

Bird 2, although obtaining the best territory, would still have lower total fitness than the highest quality bird 1 because it pays a much higher total cost for its 'dishonest' earliness. In an evolutionarily stable arrival order, a superior bird should always win in terms of total payoff. Otherwise, it would pay for it to switch to the strategy of the inferior winner, where it would gain the same benefits but have lower costs than the weaker competitor, i.e. have higher total fitness. This logic of dominance applies to all cases of condition-dependent allocation strategies (Kokko 1997, 1998 discusses dominance in the context of trade-offs between sexual advertisement and survival).

The game can be extended to an arbitrarily large number of birds and territories, by working backwards from $t = \max_i t_i^*$. At each territory position j and at time t , the maximum time Δt that an individual i is willing to advance its arrival is obtained by balancing the advantage that the next-best territory gives with the cost: $C_i(t - \Delta t) - C_i(t) = B_{j+1} - B_j$. The

bird with the smallest Δt (i.e. the one with highest marginal cost) will accept $B(j)$ at time t , while others advance their arrival to $t - \Delta t$. Arrival time distributions can then be generated for any distribution of territory values and cost functions (Figs 3,4).

Large gaps in the territory value distribution bring about intense competition for all territories exceeding the gap (as exemplified in the large difference between B_2 and B_3 in Fig. 2). A very prominent gap is established if the number of birds exceeds the number of suitable territories. In the model, this can be handled by setting the gain B_i to zero for birds who fail to obtain a breeding territory. When 30 new competitors are added to a population of 100 breeders and 100 territories, the arrival time distribution shifts towards much earlier dates (Fig. 3). The risk of remaining a floater intensifies competition among the breeding population, although floaters who know their relative quality will not arrive earlier than t_i^* (if they arrive at all; another possibility for nonbreeding migratory birds is to spend

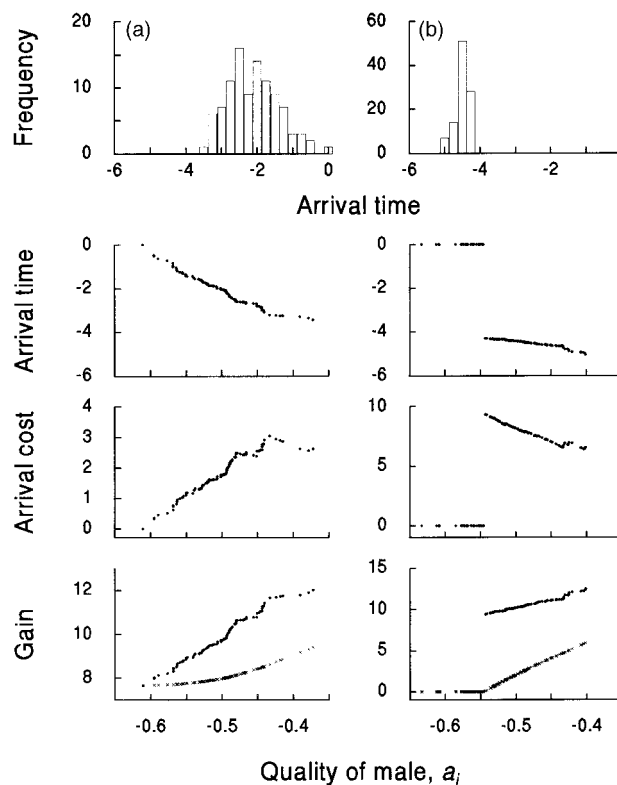


Fig. 3. The priority game for 100 territories with value distribution $\sim N(10,1)$. Birds have qualities described by a parameter $a_i \sim N(-0.5, 0.05^2)$, which determines the cost of early arrival: $C_i(t) = \exp(a_i t) - 1$ for $t < 0$ (it is assumed that the cost increases thereafter). The cost-minimizing arrival time is $t_i^* = 0$ for all a_i . Large negative values of a imply a high cost of advancing the arrival date to $t < 0$. The panels show: (1) the equilibrium frequency distribution of arrival times, based on the priority game with cascading threats; (2) individual arrival times for birds of different qualities a_i ; (3) individual costs paid at equilibrium; and (4) the individual gain (●, benefit from the territory obtained; ×, net benefit including arrival cost). (a) 100 birds compete for the 100 territories, and all birds arrive between $t = -4$ and $t = 0$. (b) 130 birds compete for 100 territories, and the whole breeding population arrives before $t = -4$. The net fitness of breeding individuals shows much higher variation if there are floaters than if not: net gain range is approximately 8–10 in (a), but 0–5 in (b).

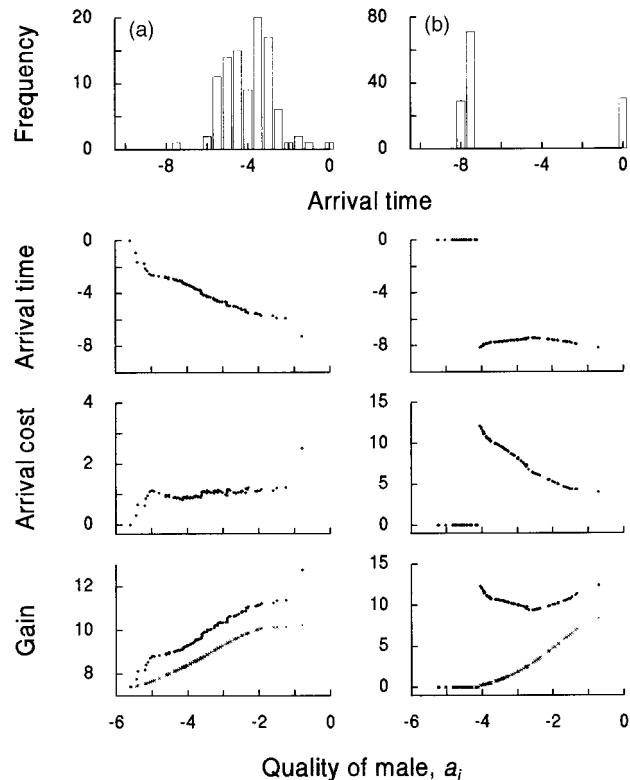


Fig. 4. The priority game as in Fig. 3, but with a cost function as in Fig. 2(b), which may give larger marginal costs for higher quality individuals. The quality parameter a_i determines the cost function such that large negative a_i values imply slow decreases in the cost: $C_i(t) = \exp[-(t + 10)/2] + \exp\{-(t + 10)/4\}^{a_i}$ for $-10 < t < 0$. As in the example of Fig. 3, it is assumed that the cost increases after the minimum point $t^* = 0$. The floater-free case (a) predicts an honest arrival order, as arrival is not early enough to give rapid increases in the marginal costs of highest quality individuals. However, when 30 floaters are introduced to compete for the 100 territories (b), arrival time shifts to a point where some lower quality individuals arrive before their superior competitors, and arrival order has a nonlinear relationship to individual condition (b2). However, net gain is still highest for best competitors (b4) (●, benefit from the territory obtained; ×, net benefit including arrival cost).

their summer in the overwintering areas, Alerstam 1990). Moreover, because of a large gap between the floater and territorial payoff, compared to value differences between breeding territories, the whole breeding population will arrive almost synchronously (Fig. 3b).

Both with and without floaters, breeding individuals in worst condition will end up in lowest quality territories, but if floaters force them to occupy these sites almost as early as the prime sites, they also pay the highest costs of arrival. Hence, the net fitness of breeding individuals shows much higher variation if there are floaters than if there are none (compare the net gain range, approximately 8–10 in Fig. 3a, to the range of 0–5 in Fig. 3b).

Introducing a cost function which allows for ‘dishonest’ arrival orders does not necessarily alter the order too much (Fig. 4). Arrival time may still be related to condition as competition does not necessarily reach levels where order reversals occur (Fig. 4a). Intensifying competition by adding floaters

can generate examples where arrival order does not strictly correspond to the condition order (Fig. 4b), but dishonesty remains slight as the competition leads to almost synchronous arrival of breeders.

Extensions of the priority game

The priority game as described above is simple, deterministic and somewhat abstract. This section investigates two extensions which add realism to the model. First, the assumption is relaxed that each arriving bird has perfect knowledge of the values of all available territories. The second enhancement redefines the arrival cost to assume the form of early spring mortality at the time of arrival; here, territories of dead birds are vacated for the later arrivals to use.

The previous sections assume that arriving birds have perfect knowledge of the values of different territories and can sample all relevant sites to find the best one. If sampling of territories is limited, later-arriving birds may obtain a better territory by chance, if it has remained unnoticed by the earlier birds. This will reduce the benefits of early arrival compared to the 'perfect knowledge' model.

Consider again the simplest case of two birds arriving at two territories, B_1 and B_2 , but replace B_2 by two separate territories B_{21} and B_{22} , which have the average quality B_2 [i.e. $(B_{21} + B_{22})/2 = B_2$]. Furthermore, assume that each bird can sample two territories before deciding where to settle; if one of these is already occupied there is no choice but to settle on the free one. Instead of the earlier-arriving bird always obtaining B_1 and the second one obtaining B_2 , there are now several possibilities of occupation patterns for the first- and second-arriving birds:

B_1	B_{21}	B_{22}	Probability
1	2	—	$\frac{2}{3} \cdot \frac{2}{3}$
1	—	2	$\frac{2}{3} \cdot \frac{1}{3}$
2	1	—	$\frac{1}{3} \cdot \frac{2}{3}$
2	—	1	0
—	1	2	$\frac{1}{3} \cdot \frac{1}{3}$
—	2	1	0

The first row arises from recognizing that the probability of the first-arriving bird finds territory B_1 is $2/3$, after which there is a $2/3$ probability that the samples of the second bird contain the next best option, B_{21} . Other rows are similarly derived.

The expected benefits are

$$\frac{6}{9} B_1 + \frac{2}{9} B_{21} + \frac{1}{9} B_{22}$$

and

$$\frac{2}{9} B_1 + \frac{4}{9} B_{21} + \frac{3}{9} B_{22}$$

for the first and second bird, respectively. The benefit obtained by being first is therefore

$$\frac{4}{9} \left(B_1 - \frac{B_{21} + B_{22}}{2} \right) = \frac{4}{9} (B_1 - B_2).$$

The analysis of the game is equivalent to the original priority game, but the benefit obtained by arriving earlier than a competitor is decreased from $B_1 - B_2$ to $4/9 (B_1 - B_2)$. Hence the likelihood that the Stackelberg date T_S is reached is diminished [as it requires smaller costs $C_2(t)$], and the time difference T_S required to keep the second bird behind is smaller. Similar arguments should apply for larger populations as well. Arriving later than another

individual always means a reduced expectation of the territory value, but if the number of potential territories is large compared to the number of birds and their sampling capacity, the expected reduction is small and may become negligible if birds rarely meet to compete for the same territories. As competition weakens and vanishes, T_S approaches t^* .

In reality, however, useful habitats are predicted to become saturated, to the extent that in areas of sufficiently high reproductive output the majority of a population is predicted to exist in a floater status (Kokko & Sutherland 1998). Because this predicts considerable failure prospects for obtaining a suitable territory, competition for earliness is likely to be abundant, with the majority of individuals in any migratory population paying its costs. Also, if arriving birds compete locally for a limited number of territories, of which they can sample a large fraction, the effects of stochasticity remain limited.

REOCCUPATION OF TERRITORIES AFTER DEATH OF THE OWNER

Another complication of the priority game is that the cost of early arrival may be more than an abstract reduction in fitness. As it is likely to be a risk of death (Møller 1994b), it may have the side-effect of rendering vacant the territory that others are interested in. To investigate this alternative, the priority game is reformulated in terms of explicit survival probabilities. It is assumed that there is an optimum arrival time t_i^* for each bird which produces maximum survival, $s_i(t_i^*)$. The benefit of an early-arriving bird is now scaled by the probability that the bird survives to gain the benefit. The gain of bird 1 arriving first is therefore $s_1(t) B_1$; if bird 2 arrives first, the benefit is $s_2(t) B_1$. For shorthand notation the scaling $B_2 = 1$ and $B_1 = b > 1$ will be used.

If the first bird died at the time of its arrival, the second is assumed to take over its territory. The second bird also gains any benefit only if he survives his arrival. The expected gain for bird 1 or 2 that comes second is therefore $s_1(t) \{ [1 - s_2(t)]b + s_2(t) \}$ or $s_2(t) \{ [1 - s_1(t)]b + s_1(t) \}$, respectively.

There is no simple graphical solution available as in the previous versions of the game, but calculations are performed likewise. I present solutions for the simple case where $t_1^* = t_2^*$; other cases are similarly derived. When $t_1^* = t_2^* = t^*$, both birds would benefit from arriving slightly earlier than the other. For bird 1 to deter bird 2 it has to choose an arrival time T_{S1} where:

$$s_2(T_{S1}) b = s_2(t^*) \{ [1 - s_1(T_{S1})] b + s_1(T_{S1}) \}$$

$$\iff \frac{s_2(t^*) - s_2(T_{S1})}{s_2(t^*)} = s_1(T_{S1}) \frac{b - 1}{b} \quad \text{eqn 1}$$

The lefthand side of this equation decreases from 1 [when sufficiently long timespans $t < 0$ are consid-

ered to give $s_2(t) \rightarrow 0$), to value 0 when $t = t^*$. The righthand side increases from 0 to $s_1(t^*)(b-1)/b > 0$ when $t = t^*$. Hence there is a unique date T_{S1} which will suffice to deter bird 2. It moves towards earlier dates when the difference in territory qualities b is increased.

However, by a similar argument, one can show that there also exists a point T_{S2} which would deter bird 1, if used by bird 2. Reversing the role of birds in equation 1 gives the condition for T_{S2} :

$$\frac{s_1(t^*) - s_1(T_{S2})}{s_1(t^*)} = s_2(T_{S2}) \frac{b-1}{b} \quad \text{eqn 2}$$

The point T_{S2} may be earlier or later than T_{S1} (Figs 5, 6). A mere definition of smaller survival in the inferior individual therefore does not determine the arrival order; one has to find out which bird will be more easily deterred. It is easy to show that this is determined by the order of the solutions T_{S1} and T_{S2} : the later solution will always be in use. Bird 1 will use T_{S1} if it gains a net benefit by doing so, i.e. if it does better by choosing T_{S1} than arriving later than bird 2:

$$s_1(T_{S1}) b > s_1(t^*) [1 - s_2(T_{S2}) b + s_2(T_{S2})] \\ \Leftrightarrow \frac{s_1(t^*) - s_1(T_{S1})}{s_1(t^*)} < s_1(T_{S1}) \frac{b-1}{b} \quad \text{eqn 3a}$$

Likewise, bird 2 will use T_{S2} only if:
 $s_2(T_{S2}) b > s_2(t^*) [1 - s_1(T_{S1}) b + s_1(T_{S1})]$

$$\Leftrightarrow \frac{s_2(t^*) - s_2(T_{S2})}{s_2(t^*)} < s_2(T_{S1}) \frac{b-1}{b} \quad \text{eqn 3b}$$

The righthand sides of inequalities (eqn 3a–b) can be replaced by the equation defining T_{S1} and T_{S2} (eqns 1–2), which gives the criteria:

T_{S1} in use if
 $\frac{s_1(t^*) - s_1(T_{S1})}{s_1(t^*)} < \frac{s_1(t^*) - s_1(T_{S2})}{s_1(t^*)} \Leftrightarrow T_{S1} > T_{S2}$
[because $s_1(t^*) > 0$],

T_{S2} in use if
 $\frac{s_2(t^*) - s_2(T_{S2})}{s_2(t^*)} < \frac{s_2(t^*) - s_2(T_{S1})}{s_2(t^*)} \Leftrightarrow T_{S1} < T_{S2}$
[because $s_2(t^*) > 0$].

Hence, the later solution is always in use, and the possibility for ‘dishonest’ arrival orders remains, if $T_{S2} > T_{S1}$ (Figs 5, 6). Arrival order can be honest only if the inequality:

$$\frac{s_2(t^*) - s_2(T_{S2})}{s_2(t^*)} > \frac{s_1(t^*) - s_1(T_{S1})}{s_1(t^*)} \quad \text{eqn 4}$$

applies, i.e. if the inferior bird loses a larger fraction of its survival if it advances arrival from t^* to T_{S2} ,

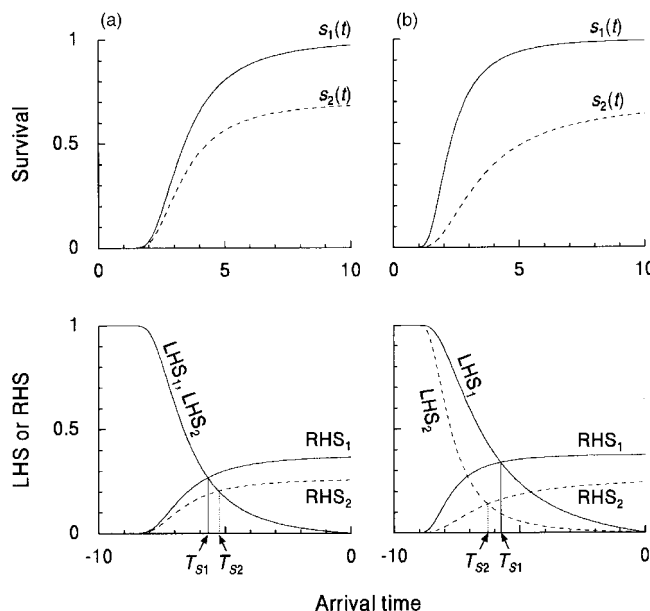


Fig. 5. Solutions of the two-bird game with spring mortality. The upper row gives the assumed survival functions according to arrival time, and the lower row depicts the solution of equations 1 and 2. The Stackelberg arrival time T_{S1} for bird 1 is found where the lefthand side $LHS_1 = [s_2(t^*) - s_2(t)]/s_2(t^*)$ equals the righthand side $RHS_1 = s_1(t) (b-1)/b$ of equation 1; similarly for T_{S2} . Only the later Stackelberg arrival time will be in use. (a) Survival of bird 2 is smaller than that of bird 1, leading to $RHS_2 < RHS_1$. It has the same shape, however, so that the proportional costs described by LHS_1 and LHS_2 are equal. This causes T_{S2} to be the later Stackelberg arrival time. (b) Survival functions differ in shape, in that bird 1 initially loses less of its survival when advancing arrival from $t^* = 0$. Therefore, $LHS_2 < LHS_1$, which restores the honesty of the arrival orders: T_{S1} being later than T_{S2} will be the one in use, and bird 2 will arrive at $t^* = 0$.

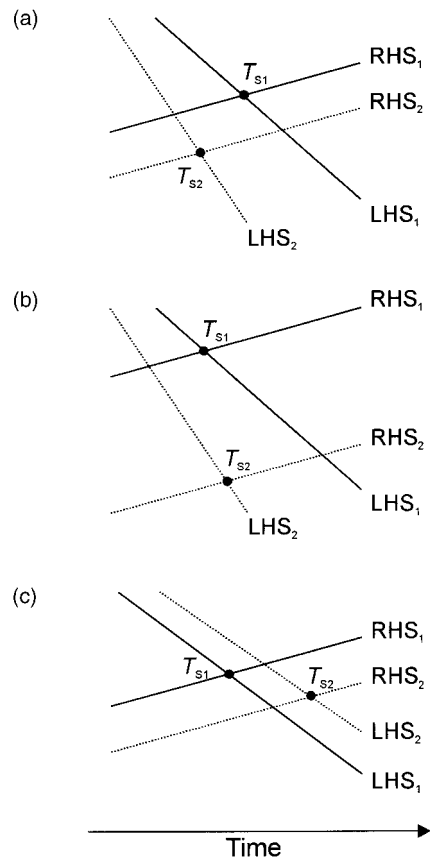


Fig. 6. Three possible configurations of the Stackelberg arrival dates T_{S1} and T_{S2} in the two-bird game with vacating territories. LHS and RHS curves show solutions to equations 1 and 2 as in Fig. 5. (a) If the differential cost criterion applies ($LHS_2 < LHS_1$), arrival order can be honest: $T_{S1} > T_{S2}$ makes bird 1 use its Stackelberg date, and bird 2 moves to the cost-minimizing t^* . This requires that the survival difference is not large, indicated by RHS_1 and RHS_2 being near each other. (b) The differential cost criterion does not suffice to make T_{S1} appear later than T_{S2} , if the difference in survival is too large, indicated by a large gap between RHS_1 and RHS_2 . (c) If the differential cost criterion is not fulfilled, i.e. if $LHS_2 \geq LHS_1$, arrival order will be always dishonest: T_{S2} is now bound to be later than T_{S1} because $RHS_2 < RHS_1$ by definition. This makes bird 2 use its Stackelberg arrival time T_{S2} and bird 1 arrive late at the cost-minimizing t^* .

than the superior bird by advancing from t^* to T_{S1} (Fig. 5). This is the differential cost criterion applied to the priority game with mortality, and it is necessary but not sufficient to ensure honest arrival order. Even if the inferior bird loses survival faster, its T_{S2} can remain larger than T_{S1} if its survival is low anyway (Figs 5b, 6b). A very low-quality bird may adopt a high-risk strategy with small success chances, but large potential payoffs (see Kokko 1997 for similar strategies in sexual signalling).

Hence, arrival order is predicted to be honest if the superior bird suffers a smaller relative change in its survival when it advances its arrival date, and if

birds do not differ very much in their overall survival prospects (scaled by the relative difference in territory values). If this holds true, the prediction of the priority game remains robust even if deaths of early-arriving birds are allowed for: birds that suffer relatively more from advancing their arrival date should arrive at their cost-minimizing optima, and their superior competitors should arrive sufficiently early to ensure their priority.

Discussion

The priority game predicts considerable advancing of arrival dates in migratory populations, whenever individuals have to take into account competition for prime breeding sites (or other priority-dependent advantages of early arrival), in addition to the seasonal effects that determine optimal onset of breeding activities. The model also predicts state-dependence of arrival times: individuals that suffer more from advancing their arrival date from their cost-minimizing optimum should do so to a lesser degree.

The finding that arrival orders will be condition dependent if costs of advancing arrival are higher for individuals in lower condition is hardly surprising, given the intuitive appeal of this reasoning (e.g. Møller 1994a,b). Early individuals often have telltale signs of their superiority such as stronger sexual signalling: early males sing more in willow warblers [*Phylloscopus trochilus* (L.)] (Arvidsson & Neergaard 1991; Nyström 1997), blackcaps [*Sylvia atricapilla* (L.)] (Hoi-Leitner, Nechtelberger & Dittami 1993) and pied flycatchers [*Ficedula hypoleuca* (Pall.)] (Lampe & Espmark 1994); early pied flycatchers are also brightest in colour (Slagsvold & Lifjeld 1988). Old males also often arrive before second-year birds (Hill 1989; Woodrey & Chandler 1997; Hasselquist 1998; Hockey, Turpie & Velásquez 1998). Møller (1994b) provides direct evidence that male barn swallows [*Hirundo rustica* (L.)] of high quality have a lower mortality cost of early arrival, and that the variance in arrival date increases under poor environmental conditions, when the costs of early arrival are high. In this species, a measure of condition (haematocrit) is related to both arrival date and sexual display (Saino *et al.* 1997a,b).

However, the mere 'costliness' itself turns out not to suffice to bring about honest condition-dependence in the arrival order. Rather, *marginal* costs of advancing the date further always have to be higher for low-quality birds to ensure the honest ordering of individuals. This corresponds to the requirement of differential costs for individuals of different qualities in the context of handicap signalling (Grafen 1990). In the current context, arrival order reversals are possible if cost shapes resemble Fig. 2(b), where differences in costs experienced by high and low

quality males disappear at very early arrival. Further, the criterion of differential costs is a necessary but insufficient condition for honest ordering, if a too early arrival can lead to the death of a territory owner, which leaves the territory vacant for his subsequent rivals.

Best individuals should always end up having highest fitness, but the composition of this into costs paid and gains obtained may vary. High quality birds pay highest costs if arrival times are widely spaced. However, competition will intensify if there are large 'gaps' in the distribution of territory values, which happens especially if the habitat saturates such that an individual arriving too late cannot breed at all. Cascading competition will then lead to almost synchronous arrival, and individuals of low condition will suffer the highest costs of arriving as early as they can possibly afford to.

A central feature of the model is that almost all individuals will pay higher costs because of the addition of new competitors. Migratory populations living in saturated habitats should therefore advance their arrival more, and pay larger costs for doing so, than those in which individuals do not face a risk of remaining a floater. There are also interesting implications considering yearly fluctuations in the environment or population size and individually optimal strategies. An obvious prediction is that individuals should arrive later if the cost of achieving a specific arrival date is increased. Adverse weather indeed delays migration, to the extent that birds may turn back on their route when encountering bad enough conditions (Richardson 1978). A perhaps less obvious prediction is that arrivals should become earlier and more synchronized in years of high population density, if the number of potential territories remains constant. Whether or not this is possible depends on whether birds have knowledge of the population size at the end of the winter or during spring migration. Achieving this may be difficult especially in long-distance migrants, as the knowledge should concern the local density in the area where the individual is going to settle.

To obtain a good overview of the problem of migration decisions, one should link the evolutionarily stable arrival dates with considerations of optimal migration scheduling, including possibly state-dependent choices of wintering areas (Myers 1981), the optimal use of stopover sites to manage flight fuelling (Weber, Houston & Ens 1994; Weber & Houston 1997; Weber, Ens & Houston 1998), and optimal responses to stochastic events such as varying weather (Williams & Nichols 1984). It is often found that old males precede young males and females already on stopover sites (Francis & Cooke 1986), which suggests that they depart earlier (Nisbet & Wedway 1972) and/or winter nearer the breeding grounds (Myers 1981); late individuals may

also compensate by migrating faster (Fransson 1995). For the current purpose, the outcome of decisions made during migration can be summarized into the form of a condition-dependent trade-off between arrival date and cost paid to achieve that date. Interestingly, willow warbler males do not deplete all their body fat storage to arrive at their breeding sites as early as possible (Fransson & Jakobsson 1998), and redpolls [*Carduelis flammea* (L.)] show a similar pattern (Romero *et al.* 1997). These findings suggest that birds need to balance their body condition at arrival to aid subsequent breeding activities, and hence provide a further example that birds need to take various costs of advancing arrival dates into account to avoid paying too high costs in the priority game.

The timespan of the model can be extended backwards to cover the whole wintering season, which has implications for the evolution of partial migration. If costs of advancing arrival into the wintering season remain limited enough for birds of highest quality, it may pay for them to remain resident throughout the winter. This predicts that partial migration can result from competition for high quality territories, and that birds of high quality should be more prone to use the nonmigratory strategy, especially so if the autumn population density is high. A complete analysis of this problem would require taking into account the density-dependent effects of resident numbers on overwintering survival, as these can also explain the coexistence of migratory and nonmigratory strategies (Kaitala, Kaitala & Lundberg 1993).

This paper considers two additions (effects of limited sampling and deaths of territorials) to the simple game, finding that predictions are generally robust. At least two further complications exist. First, arrival orders may become more complicated if territory ownership is not simply settled by priority, but if later-arriving individuals can challenge territorial birds (Broom, Cannings & Vickers 1996, 1997). Whether or not this will disturb the original arrival order will depend on the probabilities of success for the challenger. Broom *et al.* (1996, 1997) show that the evolutionarily stable order of territory acquisition in n identical birds can become very complicated, but their model nevertheless predicts ordered arrival with little conflict if the success probability of a territorial challenge is low. Many studies suggest strong benefits of prior ownership (Krebs 1982; Rohwer 1982; Jakobsson 1988; Bortolotti & Iko 1992; Tobias 1997). In the view of the present model, birds of highest condition arrive first or almost first under very general conditions, and it is then unlikely that late, low quality newcomers can take over their territories (see also Nyström 1997). Challenges might be more likely to be successful in scenarios where the condition-

dependent arrival order includes order reversals, but the prospect of losing a territory might then be sufficient to deter a low-quality individual from 'dishonestly' early arrival, which would again restore honest arrival orders.

A second but less severe restriction of the priority game is that the benefit of early arrival is defined as an increase in the value of the territory obtained. Other benefits are possible: early arrival may enhance breeding success as it shortens the time needed to acquire a mate and start breeding (Møller 1994a,b; Rowe *et al.* 1994) or increases the quality of the mate obtained (Darwin 1871, pp. 261–262; Alatalo, Lundberg & Ståhlbrand 1984; Arvidsson & Neergaard 1991; Lozano *et al.* 1996); in these cases, enhanced success is often primarily based on territory quality (e.g. Alatalo, Lundberg & Glynn 1986; Hasselquist 1998). Earliness may also increase a male's extra-pair success (Langefors, Hasselquist & von Schantz 1998) or his chances of becoming polygynous (Hasselquist 1998). Whatever the form of the advantage, the benefit of early arrival can be interpreted to be covered by the model formulation as long as it is dependent on priority: benefits B_j then simply incorporate the advantages of rapid pairing with high quality mates, in addition to the direct benefits of superior resources. Hence, the validity of the model is quite general regarding priority benefits. 'Cascading' competition should arise whenever priority brings about benefits, and it therefore applies to sexual selection in monogamous species even if nonterritorial (Darwin 1871; Kirkpatrick, Price & Arnold 1990), or to resident species which establish territories in the spring.

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References

- Alatalo, R.V., Lundberg, A. & Ståhlbrandt, K. (1984) Female mate choice in the pied flycatcher *Ficedula hypoleuca*. *Behavioral Ecology and Sociobiology*, **14**, 253–261.
- Alatalo, R.V., Lundberg, A. & Glynn, C. (1986) Female pied flycatchers choose territory quality and not male characteristics. *Nature*, **323**, 152–153.
- Alerstam, T. (1990) *Bird Migration*. Cambridge University Press, Cambridge.
- Arvidsson, B.L. & Neergaard, R. (1991) Mate choice in the willow warbler—A field experiment. *Behavioral Ecology and Sociobiology*, **29**, 225–229.
- Bortolotti, G.R. & Iko, W.M. (1992) Non-random pairing in American kestrels: Mate choice versus intra-sexual competition. *Animal Behaviour*, **44**, 811–821.
- Broom, M., Cannings, C. & Vickers, G.T. (1996) Choosing a nest-site—contests and catalysts. *American Naturalist*, **147**, 1108–1114.
- Broom, M., Cannings, C. & Vickers, G.T. (1997) A sequential-arrivals model of territory acquisition. *Journal of Theoretical Biology*, **189**, 257–272.
- Bulmer, M.G. (1983a) Models for the evolution of protandry in insects. *Theoretical Population Biology*, **23**, 314–322.
- Bulmer, M.G. (1983b) The significance of protandry in social hymenoptera. *American Naturalist*, **121**, 540–551.
- Crick, H.Q.P., Dudley, C., Glue, D.E. & Thomson, D.L. (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.
- Daan, S. & Tinbergen, J.M. (1997) Adaptation of life histories. *Behavioural Ecology: an Evolutionary Approach* (eds Krebs, J.R. & Davies, N.B.), pp. 311–333, 4th edn. Blackwell Science Ltd, Oxford.
- Daan, S., Dijkstra, C. & Tinbergen, J.M. (1990) Family planning in the Kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour*, **114**, 83–116.
- Darwin, C. (1871) *The Descent of Man, and Selection in Relation to Sex*. Murray, London.
- Enstrom, D.A. (1992) Delayed plumage maturation in the orchard oriole (*Icterus spurius*): Tests of winter adaptation hypotheses. *Behavioral Ecology and Sociobiology*, **30**, 35–42.
- Flood, N.J. (1984) Adaptive significance of delayed plumage maturation in male northern orioles. *Evolution*, **38**, 262–279.
- Francis, C.M. & Cooke, F. (1986) Differential timing of spring migration in wood warblers. *Auk*, **103**, 548–556.
- Fransson, T. (1995) Timing and speed of migration in North and West European populations of *Sylvia* warblers. *Journal of Avian Biology*, **26**, 39–48.
- Fransson, T. & Jakobsson, S. (1998) Fat storage in male Willow Warblers in spring: Do residents arrive lean or fat? *Auk*, **115**, 759–763.
- Grafen, A. (1990) Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Hasselquist, D. (1998) Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376–2390.
- Hill, G.E. (1988) The function of delayed plumage maturation in male black-headed grosbeaks. *Auk*, **105**, 1–10.
- Hill, G.E. (1989) Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? *Animal Behaviour*, **37**, 665–673.
- Hockey, P.A.R., Turpie, J.K. & Velásquez, C.R. (1998) What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *Journal of Avian Biology*, **29**, 325–330.
- Hoi-Leitner, M., Nechtelberger, H. & Dittami, J. (1993) The relationship between individual differences in male song frequency and parental care in blackcaps. *Behaviour*, **126**, 1–12.
- Iwasa, Y. & Haccou, P. (1994) ESS emergence pattern of male butterflies in stochastic environments. *Evolutionary Ecology*, **8**, 503–523.
- Iwasa, Y., Odendaal, F.J., Murphy, D.D., Ehrlich, P.R. & Launer, A.E. (1983) Emergence patterns in male butterflies: a hypothesis and a test. *Theoretical Population Biology*, **23**, 363–379.
- Jakobsson, S. (1988) Territorial fidelity of willow warbler *Phylloscopus trochilus* males and success in competition over territories. *Behavioral Ecology and Sociobiology*, **79**, 79–84.

- Kaitala, A., Kaitala, V. & Lundberg, P. (1993) A theory of partial migration. *American Naturalist*, **142**, 59–81.
- Kirkpatrick, M., Price, T. & Arnold, S.J. (1990) The Darwin–Fisher theory of sexual selection in monogamous birds. *Evolution*, **44**, 180–193.
- Kokko, H. (1997) Evolutionarily stable strategies of age-dependent sexual advertisement. *Behavioral Ecology and Sociobiology*, **41**, 99–107.
- Kokko, H. (1998) Good genes, old age and life history trade-offs. *Evolutionary Ecology*, **12**, 739–750.
- Kokko, H. & Sutherland, W.J. (1998) Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist*, **152**, 354–366.
- Krebs, J.R. (1982) Territorial defence in the great tit *Parus major*: do residents always win? *Behavioral Ecology and Sociobiology*, **11**, 185–194.
- Lampe, H.M. & Espmark, Y.O. (1994) Song structure reflects male quality in pied flycatchers, *Ficedula hypoleuca*. *Animal Behaviour*, **47**, 869–876.
- Langefors, Å., Hasselquist, D. & von Schantz, T. (1998) Extra-pair fertilizations in the Sedge Warbler. *Journal of Avian Biology*, **29**, 134–144.
- Lozano, G.A., Perreault, S. & Lemon, R.E. (1996) Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology*, **27**, 164–170.
- Lundberg, A. & Alatalo, R.V. (1992) *The Pied Flycatcher*. Academic Press, San Diego.
- Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird using stable-carbon isotopes. *Science*, **282**, 1884–1886.
- Møller, A.P. (1990) Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. *Animal Behaviour*, **39**, 458–465.
- Møller, A.P. (1994a) Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology*, **35**, 115–122.
- Møller, A.P. (1994b) *Sexual Selection and the Barn Swallow*. Oxford University Press, Oxford.
- Myers, J.P. (1981) A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology*, **59**, 1527–1534.
- Nisbet, I.C.T. & Wedway, L. (1972) Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis*, **114**, 451–494.
- Nyström, K.G.K. (1997) Food density, song rate, and body condition in territory-establishing willow warblers (*Phylloscopus trochilus*). *Canadian Journal of Zoology*, **75**, 47–58.
- Osborne, M.J. & Rubinstein, A. (1994) *A Course in Game Theory*. MIT Press, Cambridge, Massachusetts.
- Parker, G.A. & Courtney, S.P. (1983) Seasonal incidence: adaptive variation in the timing of life history stages. *Journal of Theoretical Biology*, **105**, 147–155.
- Price, T., Kirkpatrick, M. & Arnold, S.J. (1988) Directional selection and the evolution of breeding date in birds. *Science*, **240**, 798–799.
- Rasmusen, E. (1990) *Games and Information: an Introduction to Game Theory*. 2nd edn. Cambridge University Press, Cambridge.
- Richardson, W.J. (1978) Timing and amount of bird migration in relation to weather: a review. *Oikos*, **30**, 303–310.
- Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531–546.
- Romero, L.M., Soma, K.K., O'Reilly, K.M., Suydam, R. & Wingfield, J.C. (1997) Territorial behavior, hormonal changes, and body condition in an arctic-breeding song bird, the redpoll (*Carduelis flammea*). *Behaviour*, **134**, 727–747.
- Rowe, L., Ludwig, D. & Schluter, D. (1994) Time, condition and the seasonal decline of avian clutch size. *American Naturalist*, **143**, 698–722.
- Saino, N., Cuervo, J.J., de Ninni, P., Lope, F. & Møller, A.P. (1997a) Haematocrit correlates with tail ornament size in three populations of the Barn Swallow (*Hirundo rustica*). *Functional Ecology*, **11**, 604–610.
- Saino, N., Cuervo, J.J., de Krivacek, M., Lope, F. & Møller, A.P. (1997b) Experimental manipulation of tail ornament size affects the hematocrit of male barn swallows (*Hirundo rustica*). *Oecologia*, **110**, 186–190.
- Slagsvold, T. & Lifjeld, J.T. (1988) Plumage colour and sexual selection in the pied flycatcher *Ficedula hypoleuca*. *Animal Behaviour*, **36**, 395–407.
- Svensson, E. (1997) Natural selection on avian breeding time: Causality, fecundity-dependent, and fecundity-independent selection. *Evolution*, **51**, 1276–1283.
- Tobias, J. (1997) Asymmetric territorial contests in the European robin: the role of settlement costs. *Animal Behaviour*, **54**, 9–21.
- Verboven, N. & Visser, M.E. (1998) Seasonal variation in local recruitment of great tits: the importance of being early. *Oikos*, **81**, 511–524.
- Verhulst, S. & Tinbergen, J.M. (1991) Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. *Journal of Animal Ecology*, **60**, 269–282.
- Wang, G.Y., Greenfield, M.D. & Shelly, T.E. (1990) Intermale competition for high-quality host-plants: The evolution of protandry in a territorial grasshopper. *Behavioral Ecology and Sociobiology*, **27**, 191–198.
- Weber, T.P. & Houston, A.I. (1997) Flight costs, flight range and the stopover ecology of migrating birds. *Journal of Animal Ecology*, **66**, 297–306.
- Weber, T.P., Houston, A.I. & Ens, B.J. (1994) Optimal departure fat loads and stopover site use in avian migration: an analytical model. *Proceedings of the Royal Society of London B*, **258**, 29–34.
- Weber, T.P., Ens, B.J. & Houston, A.I. (1998) Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology*, **12**, 377–401.
- Wiggins, D.A., Pärt, T. & Gustafsson, L. (1994) Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. *Oikos*, **70**, 359–364.
- Wiklund, C. & Fagerström, T. (1977) Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. *Oecologia*, **31**, 153–158.
- Williams, B.K. & Nichols, J.D. (1984) Optimal timing in biological processes. *American Naturalist*, **123**, 1–19.
- Woodrey, M.S. & Chandler, C.R. (1997) Age-related timing of migration: geographic and interspecific patterns. *Wilson Bulletin*, **109**, 62–67.

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