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Predicting conditions for migration: effects of density dependence and habitat quality

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Migration is widespread among animals, but the factors that influence the decision to migrate are poorly understood. Within a single species, populations may be completely migratory, completely sedentary or partially migratory. We use a population model to derive conditions for migration and demonstrate how migratory survival, habitat quality and density dependence on both the breeding and non-breeding grounds influence conditions for migration and the proportion of migrants within a population. Density dependence during the season in which migratory and sedentary individuals use separate sites is necessary for partial migration. High levels of density dependence at the non-shared sites widen the range of survival values within which we predict partial migration, whereas increasing the strength of density dependence at the shared sites narrows the range of survival values within which we predict partial migration. Our results have important implications for predicting how contemporary populations with variable migration strategies may respond to changes in the quality or quantity of habitat.

Keywords: partial migration; habitat loss; population dynamics

1. INTRODUCTION

Annual migration is a widespread adaptation to seasonally varying environments, but the factors that influence the decision to migrate are poorly understood. Within a species, populations may be completely migratory, completely sedentary or partially migratory. Partial migration, where some individuals within the population migrate and others do not, occurs in a wide array of taxa including insects, fishes and birds (Lundberg 1988; Dingle 1996). Breeding experiments demonstrate that migratory behaviour in birds can be selected for, or against, in few generations (Berthold *et al.* 1990; Berthold 2003), suggesting that degree of migration in natural populations can be rapidly influenced by environmental or demographic factors.

The degree of migration within a population may depend on the availability of suitable sites, the costs associated with migration (Alexander 1998) or the level of competition between residents and migrants (Lundberg 1988). Early studies suggested that partial migration could be driven by environmental stochasticity (Cohen 1967; Alerstam & Enckell 1979; Lundberg 1987), but the model of Kaitala *et al.* (1993) suggests that stochasticity by itself is not sufficient to maintain partial migration. Instead, models show that, in a uniform habitat, density-dependent vital rates can drive the evolution and maintenance of partial migration (Lundberg 1987, 1988; Kaitala *et al.* 1993).

Our goal is to examine the conditions that are necessary to produce complete migration, complete residency or partial migration for a population in an unvarying environment and to show how the survival cost of migration affects these conditions. We assume that migration is genetically determined and that both survival and breeding success are density dependent. We use an equilibrium population model to derive the range of parameter values within which we predict different migration strategies to occur and use this model to explore how habitat loss and degradation affects conditions for migration.

2. MODEL DESCRIPTION

We consider a population of R residents and M migrants. Residents spend their non-breeding (winter) and breeding seasons at the same site, whereas migrants spend the non-breeding season at the same site as residents but migrate to a distant breeding site. Both strategies are inherited and we assume that each strategy is completely heritable; all offspring from migrant parents are migrants and vice versa. With small changes, this model framework could also be applied to the reverse situation where residents and migrants share the same breeding site. The results hold for either situation.

At time t, at the beginning of the non-breeding season, we have R_t residents and M_t migrants. Survival during winter is given by a density-independent *per capita* survival d that is reduced linearly by a density-dependent term d' multiplied by number of birds present. The number of residents at the end of the winter $R_{t+(1/2)}$ is given by

$$R_{t+(1/2)} = R_t(d - d'(M_t + R_t)). \qquad (2.1)$$

We assume that migrants arrive later and, therefore, experience reduced competitive ability during winter (e.g. Adriaensen & Dhondt 1990; Perez-Tris & Telleria 2002). We model this by including a parameter $\delta \geq 1$, representing asymmetric competition. The number of migrants at the end of the winter $M_{t+(1/2)}$ is given by

$$M_{t+(1/2)} = M_t(d - \delta d'(M_t + R_t)). \qquad (2.2)$$

Reproductive output is similarly modelled with a density-independent (b_{R} for residents and b_{M} for migrants) and a density-dependent component (b'_{R} for residents and b'_{M} for migrants). At the beginning of the next winter, the number of residents and migrants is given by

$$R_{t+1} = R_{t+(1/2)}(b_{\mathrm{R}} - b'_{\mathrm{R}} R_{t+(1/2)}), \qquad (2.3)$$

$$M_{t+1} = M_{t+(1/2)}(b_{\mathrm{M}} - b'_{\mathrm{M}} M_{t+(1/2)})(S). \qquad (2.4)$$

$0 \leq S \leq 1$ is density-independent *per capita* survival during both spring and autumn migration combined.

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Table 1. Parameters and values used in the model. (Density-dependent values based on Sutherland (1998).)

parameter	default value	description
d	0.995	density-independent *per capita* survival (winter)
d'	0.00005	density-dependent *per capita* survival (winter)
δ	1.01	degree of asymmetric competition (winter)
b_R	2.0	density-independent *per capita* breeding success at resident site
b'_R	0.0001	density-dependent *per capita* breeding success at resident site
b_M	3.0	density-independent *per capita* breeding success at migratory site
b'_M	0.0001	density-dependent *per capita* breeding success at migratory site
S	n.a.	density-independent *per capita* survival during migration

All parameters are shown in table 1. Substituting (2.1) and (2.2) and into (2.3) and (2.4) gives

$$M_{t+1} = M_t S(d - \delta d'(M_t + R_t))(b_M - b'_M(M_t(d - \delta d'(M_t + R_t)))), \tag{2.5}$$

$$R_{t+1} = R_t(d - d'(M_t + R_t))(b_R - b'_R(R_t(d - d'(M_t + R_t)))). \tag{2.6}$$

At equilibrium, migrants are a constant proportion x of the total population and the total population size is N, thus (2.5) and (2.6) become

$$1 = S(d - \delta d'N)(b_M - b'_M xN(d - \delta d'N)), \tag{2.7}$$

$$1 = (d - d'N)(b_R - b'_R N(1 - x)(d - d'N)). \tag{2.8}$$

To derive conditions for partial migration, we first solve equations (2.7) and (2.8) simultaneously and obtain equilibrium values for x and N. For any degree of migration to occur, we set $x > 0$, and rearrange to show that one condition for partial migration is that migratory survival must exceed the following threshold,

$$S > \frac{1}{b_M(d - \delta d' N_R)}, \tag{2.9}$$

where N_R is the equilibrium population size when there are no migrants, obtained from the solution of (2.8) when $x = 0$. N_R is a function of the parameters d, d', b_R and b'_R. If S is lower than this threshold, then the entire population will be resident. The other condition for partial migration is obtained by setting $x < 1$ and rearranging to give

$$S < \frac{d' b_R^3}{(db_R - \delta d b_R + \delta)\left(d' b_R^2 b_M - b'_M(db_R - 1)(db_R - \delta d b_R + \delta)\right)}. \tag{2.10}$$

If migratory survival is higher than this threshold, then the population will be entirely migratory (figure 1*a*).

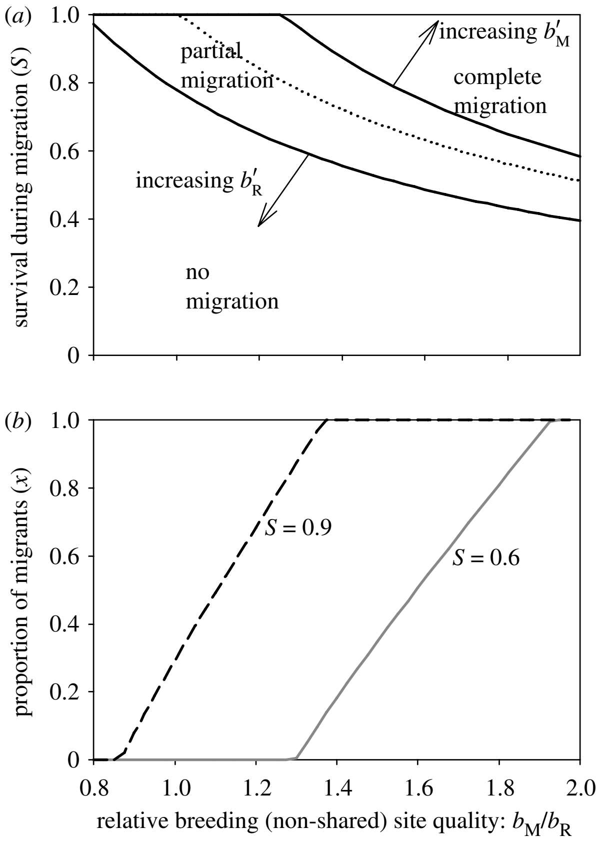

Figure 1. (*a*) Thresholds of migration survival for different migration strategies as the relative quality of migratory/resident breeding site changes. Below the lower solid line, the population is entirely resident. Above the higher solid line, the population is entirely migratory. Partial migration is predicted at survival values between the two solid lines. Parameter values are shown in table 1. The dotted line shows the boundary between residency and migration when $b'_M = 0$ and $b'_R = 0$. (*b*) Predicted proportion of migrants as the relative quality of migratory to resident breeding site changes. Dashed line shows the proportion of migrants when $S = 0.9$ and solid line shows the proportion of migrants when $S = 0.6$.

3. RESULTS

In §§§3*a*–*c*, we use the conditions (2.9) and (2.10) to show how variation in habitat quality and density dependence affects the migration strategy and the proportion of migrants x.

(a) *Effects of relative habitat quality of breeding (non-shared) sites*

As the site quality of the migratory breeding site (b_M) increases relative to the resident breeding site (b_R), the migratory survival necessary for partial and complete migration decreases (figure 1*a*) and the proportion of migrants in the population size increases (figure 1*b*). It can be seen from figure 1*a* that it is possible for partial migration to occur even when the quality of the migratory breeding site is the same or lower than the quality of the resident breeding site ($b_M \leq b_R$).

(b) *Effects of density dependence at breeding (non-shared) sites*

As expected, increasing b'_M decreases x and increasing b'_R increases x. Only the boundary between complete and partial migration is affected by changing b'_M and

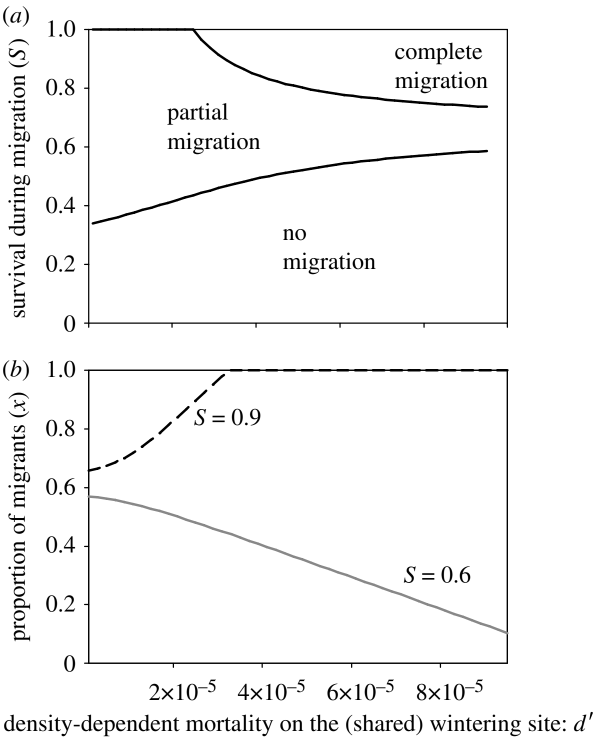

Figure 2. (*a*) Thresholds of migration survival that lead to different migration strategies as density-dependent survival on the wintering site changes. Parameter values are shown in table 1. (*b*) Proportion of migrants predicted by the model density-dependent survival on the wintering site changes. Dashed line shows the proportion of migrants when survival during migration is high ($S=0.9$) and solid line shows the proportion of migrants when survival during migration is low ($S=0.6$).

only the boundary between residency and partial migration is affected by changing b'_R.

Higher density dependence on either breeding site increases the range of survival values in which partial migration is expected to occur and lower density dependence decreases the range of survival values for partial migration. Graphically, the upper bound on figure 1*a* moves down towards the dotted line as $b'_M \to 0$ and the lower bound moves up towards the dotted line as $b'_R \to 0$. When there is no density dependence at either breeding site, the two boundaries are convergent on the dotted line and partial migration will not occur. In this case, the condition for complete migration is given by

$$S > \frac{b_R}{b_M(d\, b_R + \delta - \delta\, d\, b_R)}, \tag{3.1}$$

and the population will be completely resident if S is lower than this threshold.

(c) *Effects of density dependence during the non-breeding (shared) season*

Increasing density-dependent mortality during the non-breeding (shared) season lowers equilibrium population size and narrows the range of survival values in which we expect partial migration (figure 2*a*). Other parameters determine how the proportion of migrants (x) is affected (figure 2*b*). When S is high, increasing density dependence during winter increases x, whereas when S is low, x declines. If asymmetric competition (δ) is strong, an increase in winter competition will tend to favour the resident strategy and x will decline.

4. DISCUSSION

Fretwell (1980) asked why there are not more migratory species, given that most environments are seasonal. One explanation is that migration may be energetically expensive and impose a high mortality risk. We frame this problem in the context of population dynamics and derive thresholds of migratory survival for residency, partial migration and complete migration. We demonstrate how habitat quality and density dependence on both the breeding and non-breeding grounds influence these thresholds. Although we modelled the situation where migrants and residents share a non-breeding site and breed at different sites, our results also apply to the opposite situation where migrants and residents share a breeding site and use different over-wintering sites.

We find that density dependence during the non-shared season (the breeding season in our model) is necessary for partial migration (Kaitala *et al.* 1993). No density dependence on either of the non-shared sites leads to a single boundary between residency and complete migration, whereas increasing density dependence at either site during the non-shared season widens the range of survival values where partial migration is expected to occur. This leads to the prediction that density dependence will be stronger in partially migratory populations than in either resident or completely migratory populations.

Our results may have implications for how populations respond to changes in the quality or quantity of habitat. As in previous models (Sutherland 1998; Norris & Taylor 2006), the loss of breeding or non-breeding habitat can be represented by an increase in b' or d', respectively, and habitat deterioration can be represented by a change in b or d. If we also assume that migratory survival is inversely proportional to migration distance, our model predicts that habitat loss at the shared site will cause short-distance partially migratory populations to become completely migratory and long-distance partially migratory populations to become completely resident (figure 2*b*). If a decrease in habitat at the resident site also affects breeding success of residents (both d' and b'_R increase), then the results are more complex. The population size will decrease, but either an increase or decrease in the proportion of migrants is possible depending on other parameters, particularly the level of migratory survival and the degree of asymmetric competition (δ).

Thresholds for migration decline as the quality of the migratory site relative to the resident site (b_M/b_R) increases (figure 1*a*). Again, assuming that migratory survival is inversely related to migration distance, short-distance partially migratory populations are predicted to have lower relative difference in site quality between the non-shared sites than long-distance partially migratory populations. If migratory survival is high, density-dependent breeding success at the resident site can lead to partial migration even when the migratory breeding site is of lower quality than the resident breeding site ($b_M < b_R$). This result, which was also found by Kaitala *et al.* (1993), offers an alternative explanation to the idea that migration is a poorer strategy, practised by less competitive individuals (Adriaensen & Dhondt 1990; Able & Belthoff 1998). We also find that density dependence at the migratory site can lead to partial migration when the migratory breeding site is of higher quality than the resident breeding site ($b_M > b_R$). This is in contrast to Kaitala *et al.* (1993) who predicted that complete migration always results if the migratory site is of higher quality because they assumed that no density dependence is experienced on the migratory site.

Our model provides a framework to predict the degree of migration in animal populations either between or within species. As is true for predicting changes in abundance due to habitat loss (Sutherland 1998) and carry-over effects (Norris & Taylor 2006), one of the keys is to determine the relative strength of density dependence parameters. Unfortunately, we still lack estimates of these parameters for the vast majority of species.

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NOTICE OF CORRECTION

The abstract is now correct. 23 March 2007