

Metapopulation consequences of site fidelity for colonially breeding mammals and birds

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Summary

1. Many far-ranging bird and mammal species aggregate in colonies to breed, and most individuals remain faithful to one colony. Here, we use modelling to explore the consequences of this site fidelity for the metapopulation dynamics of such species.
2. We develop a spatially explicit model of the annual transfer process between colonies. We apply it to different spatial arrangements of 20 identical colonies and thus demonstrate that connectivity alone can, in the short term, give rise to heterogeneity in colony size.
3. We place the annual transfer model within a state-structured population model and examine the consequences of local and global density dependence for long-term dynamics. For each scenario, we investigate the implications of the strength of site fidelity, the cost of migration and the population's intrinsic growth rate.
4. Our results suggest that, under local density dependence, site fidelity slows down the colonization process and can temporarily trap the entire population in a subset of the available potential colonies. When site fidelity is strong, the metapopulation follows a step-like trajectory. Population growth occurs only rarely because individuals must overcome their site-fidelity to found new colonies. Even though this effect is temporary, it renders the entire metapopulation vulnerable to rare catastrophic collapses.
5. Under global density dependence, site fidelity imposes competition between colonies for the limiting resource. Stochastic events lead to the dominance of certain colonies and the temporary extinction of others. If site fidelity is strong, it can permanently prevent the metapopulation from occupying all available potential colonies.
6. We conclude that, irrespective of the mechanism of population regulation, colonially breeding species that show strong site fidelity are likely to occupy only a portion of the breeding habitat available to them.

Key-words: apparent carrying capacity, breeding habitat, natal dispersal, philopatry, prospecting.

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Introduction

Colonial breeding occurs in many mammals and birds. When not breeding, these animals may travel great distances, occasionally traversing the entire network of breeding colonies (e.g. McConnell *et al.* 1999). However, despite the geographical range of individuals, the

potential for complete genetic mixing is rarely achieved in colonial populations (Allen *et al.* 1995; Burg *et al.* 2003). This has been attributed to site fidelity, a behavioural characteristic common to most colonially breeding mammals and birds. However, the implications of site fidelity for population dynamics have not been investigated formally.

The existence of significant genetic differences between breeding colonies suggests that the population dynamics of colonially breeding mammals and birds should be modelled using a metapopulation approach (Harkonen & Harding 2001; Gaggiotti *et al.* 2002). In the classic metapopulation paradigm (Hanski & Gilpin

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1997) the environment consists of spatially isolated patches of suitable habitat positioned within a continuum of unsuitable habitat. However, in colonial breeders, patches (the colonies) exist only during the breeding season and habitat that is unsuitable for breeding may be suitable for other activities, such as foraging. Also, patch connectivity is not determined by physical factors such as distance or obstacles but by the animals' own behaviour. Hence, populations of colonially breeding mammals and birds are not typical metapopulations and their dynamics may not automatically follow all the conclusions of metapopulation theory.

Our objective in this paper is to adapt the metapopulation paradigm to the life history of colonial birds and mammals and to investigate how site fidelity, density dependence, intrinsic growth rate and the cost of migration affect colony occupancy and population size.

Within our general objective, we deal with two specific questions. First, we ask whether all potential colony sites will be occupied. Applied ecologists are interested in what constitutes suitable breeding habitat (Harrison 1994; Gibbs & Kinkel 1997), and occupancy is the only direct indicator of habitat suitability. Given the mobility of most colonial birds and mammals, it might be expected that colonization will proceed quickly and occupied sites be safe from extinction (Hanski, Moilanen & Gyllenberg 1996; Frederiksen & Petersen 2000). However, site fidelity may slow down the colonization process and prevent the full occupancy of a network of potential colony sites. Hence, whereas source-sink theory (Pulliam 1988; Pulliam & Danielson 1991; Watkinson & Sutherland 1995) focuses on how populations can persist indefinitely in poor-quality habitat, we are interested in whether apparently good-quality, accessible habitat can remain unoccupied indefinitely. For the sake of simplicity, we will in future refer to all potential colony sites as 'colonies' regardless of whether or not they are occupied by breeders.

Next, we ask whether occupancy patterns can be used to identify the nature of population regulation in colonially breeding species. Density dependence can operate at different spatial scales (Ray & Hastings 1996). We considered only the two extremes of the spectrum of possibilities: local and global density dependence. In nature, local density dependence arises from factors operating within each colony such as the number of potential breeding sites (Aebischer 1995; Kokko, Harris & Wanless 2004). In contrast, global density dependence results from colony-independent limitations such as the availability of food in the environment as a whole (Furness & Birkhead 1984). Because the biological mechanisms giving rise to local or global population regulation are quite different, the correct conservation and management strategy for a species will depend on the spatial scale at which population regulation operates. It would therefore be extremely valuable if the nature of density dependence could be identified from qualitative features of metapopulation dynamics.

Methods

MODELLING OVERVIEW AND STATE VARIABLES

We first construct a spatially explicit, continuous-time model for the annual redistribution of individuals between all the available colonies. We embed this into a stage-structured population model operating in discrete time under demographic stochasticity. We use a stage-structured model because most colonial birds and mammals do not become sexually mature within their first year. Hence, if it takes l years to reach sexual maturity the model has $l + 1$ classes. Newborn and immature animals are in classes zero to $l - 2$, prebreeders are in class $l - 1$ and breeders remain in class l . The total metapopulation size in a particular year τ is N_τ and the total number of animals in colony i at a time t during the year τ is $N_{\tau,i}(t)$. The sizes of different stage-classes of animals in the i th colony are $N_{\tau,i,v}(t)$ ($0 \leq v \leq l$).

MODELLING THE ANNUAL TRANSFER PROCESS

We examine the component stages of emigration, migration and settlement (Ims & Yoccoz 1997). This allows us to model the individual decisions that are involved in movement (Grosbois & Tavecchia 2003): emigration rates depend on levels of site fidelity, migration rates depend on colony connectivity, and settlement rates may depend on the performance of resident conspecifics.

Before breeding, the animals must decide whether to remain in the same colony or emigrate. This decision will be influenced by their site fidelity. Fidelity may be shown towards the site of previous, successful breeding attempts (Hoover 2003). Alternatively, it may be manifested as natal site fidelity or philopatry, the faithfulness towards an animal's natal site (Spear, Pyle & Nur 1998). Evidence, primarily for birds (Paradis *et al.* 1998) but also for colonial mammals (Pomeroy, Twiss & Redman 2000), suggests that breeding site fidelity is stronger than natal site fidelity. To simplify our model we assume that only prebreeders migrate and that their decisions are influenced by the density of visiting as well as resident animals. We use a Beverton-Holt formulation for the proportion (f) of prebreeders that decide to emigrate

$$f(N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0)) = r_F \frac{N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0)}{N_F + N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0)} \quad \text{eqn 1}$$

where $N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0)$ is the number of prebreeders and breeders in the i th colony before emigration, r_F is the maximum proportion of prebreeders that emigrate each year and N_F is the number of breeders and prebreeders at which a proportion $r_F/2$ of prebreeders emigrate.

Equation 1 is one of many possible formulations for site fidelity but it provides a compromise between simplicity and flexibility. For example, setting $N_F = 0$ and

$0 \leq r_F < 1$ gives an expression for density-independent natal site fidelity. In this case, any given animal has a probability r_F of emigrating. An alternative interpretation is that individuals have a probability of emigrating of either 0 or 1 and the proportion of animals with probability 1 is r_F . Biologically, this could arise if philopatry was inherently determined by genes that occurred with constant frequency in the population (Dingemanse *et al.* 2003). Alternatively, setting $r_F = 1$ and $N_F > 0$ gives density-dependent site fidelity. Large values of N_F lead to strong site fidelity. If $N_F = 0$ and $r_F = 1$, all prebreeders emigrate, a situation of natal site avoidance. Setting $N_F > 0$ and $0 \leq r_F < 1$ mimics a population that is a mixture of completely philopatric and partly philopatric animals. We do not examine such mixtures here, but future work could use them to quantify the evolutionary stability of different dispersal strategies.

Redistribution of prebreeders precedes the breeding season and, by default, no births occur during the transfer process. For simplicity, we also assume that any mortality occurs at the end of the transfer process. Following the decision whether or not to emigrate, the population at the i th colony will consist of a number of site-faithful animals ($M_{\tau,i}$) and a number of migrating animals ($P_{\tau,i}(t)$). The site-faithful animals will be a mixture of prebreeders and resident breeders from previous years. Because there are no deaths or births during the transfer process, $M_{\tau,i}$ remains constant and $P_{\tau,i}(t)$ changes only through movement away from and to the colony.

The flux of animals through each colony during the transfer process will depend on the number and positions of all the other colonies and the probability that a migrating animal will jump from one colony to another (Boudjemadi, Lecomte & Clobert 1999; Hanski 1999; Moilanen & Hanski 2001). We model this as a function of the distance between them. We envisage a matrix of jump probabilities:

$$\mathbf{h} = \{h_{i,j} : i, j = 1, \dots, m\} \quad \text{eqn 2}$$

where m is the total number of colonies and $h_{i,j}$ is the probability that a migrant from the i th colony jumps to the j th colony. We simulate a system of 20 colonies positioned within a square area of 100×100 units of length. We assume $h_{i,j}$ to be proportional to a function $h(d_{i,j})$ of the distance ($d_{i,j}$) between colonies i and j . Jump probabilities have been modelled previously (Neubert, Kot & Lewis 1995; Hill, Thomas & Lewis 1996; Thomas & Hanski 1997) as monotonically decreasing functions of distance, such as:

$$h(d_{i,j}) = (k + d_{i,j})^{-c} \quad \text{eqn 3}$$

We set $k = 1$ and $c = 2$. These values determine the rarity of transition events and hence the absolute rate of the colonization but do not affect the generality of our results.

For the elements of \mathbf{h} to be probabilities, the row elements of the matrix must add up to 1.

$$h_{i,j} = \frac{h(d_{i,j})}{\sum_{j=1}^m h(d_{i,j})} \quad \text{eqn 4}$$

The diagonal elements of \mathbf{h} are not zero, implying that, at any stage of the transfer process, animals can back-migrate (Boudjemadi *et al.* 1999). Further, eqn 4 introduces asymmetry in the flux of animals. Hence, although it will always be true that $h(d_{i,j}) = h(d_{j,i})$, in spatial arrangements of more than three colonies, the jump probabilities $h_{i,j}$ and $h_{j,i}$ will usually not be equal. This means that even when the numbers of animals in the colonies have approached a dynamic equilibrium, the net flow of animals between any two colonies may not be zero.

The spatial arrangement of the colonies determines the average connectivity of each. For example, in a circular arrangement, every colony has the same average distance from every other colony. In a linear arrangement, the colonies in the centre have a smaller average distance from other colonies as compared with colonies at the edges. A random arrangement may be used as a more realistic example of unequal connectivity.

The decision of a migrant to settle may or may not be density-dependent. We model the proportion (g) of migrants that decide not to settle at the colony they are currently visiting as:

$$g(N_{\tau,i,l-1}(t) + N_{\tau,i,l}(t)) = r_S \frac{N_{\tau,i,l-1}(t) + N_{\tau,i,l}(t)}{N_S + N_{\tau,i,l-1}(t) + N_{\tau,i,l}(t)} \quad \text{eqn 5}$$

The parameter r_S is the maximum settlement rate and N_S is the colony population size at which the settlement rate is $r_S/2$. Density dependence in settlement occurs for any $N_S > 0$. Biologically, this would arise if colony density affected the fitness of resident individuals (Ganter & Cooke 1998) and visiting animals used information on conspecific fitness to decide whether or not they settled at a particular breeding colony (Boulinier & Danchin 1997; Doligez, Danchin & Clobert 2002). Alternatively, setting N_S to zero results in density-independent settling.

The annual transfer model can now be stated in terms of the number of migrants in each colony ($P_{\tau,i}(t)$), the initial number of animals in each colony ($N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0)$) and the number of site faithful animals in each colony ($M_{\tau,i}$). The rate of change of migrating animals in colony i is given as the difference between incoming and outgoing animals

$$\frac{dP_{\tau,i}}{dt} = \sum_{j=1}^m h(d_{j,i}) P_{\tau,j} g(M_{\tau,j} + P_{\tau,j}) - P_{\tau,i} g(M_{\tau,i} + P_{\tau,i}) \quad \text{eqn 6}$$

$$P_{\tau,i}(0) = N_{\tau,i,l-1}(0) f(N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0))$$

where:

$$M_{\tau,i} = N_{\tau,i,l-1}(0)(1 - f(N_{\tau,i,l-1}(0) + N_{\tau,i,l}(0))) + N_{\tau,i,l}(0)$$

This system of m coupled differential equations can be solved numerically to find the numbers of animals in each colony at a certain time instant t in the year τ . If the duration of the transfer process is known (for instance, t_{\max}), then the solution of eqn 6 at t_{\max} will give the final distribution of animals before the breeding season of year τ . Alternatively it can be argued that, before breeding commences, the transfer process reaches a dynamic equilibrium and that animals have the time and information to distribute themselves 'ideally' (Fretwell & Lucas 1970; Sutherland 1983). Equilibrium solutions can be obtained by numerically solving one algebraic equation (Appendix I). This is considerably quicker than solving systems of coupled differential equations.

To illustrate some of the properties of the annual transfer model we obtain the final distribution of a fixed number of migrating animals in a circular, linear and random configuration of 20 identical colonies. To focus on the effects of connectivity on the final distribution of animals, for this particular illustration, we assume no breeding or natal site fidelity and allow all individuals to migrate.

MODELLING THE LONG-TERM METAPOPULATION DYNAMICS

We assume that the intrinsic growth rate (λ) of the population is a characteristic of the species and therefore that it can be achieved by any individual in any colony under favourable conditions. The population's intrinsic growth rate is ultimately determined by the maximum per-capita survival (s), maximum per-capita fecundity (b) and the age to recruitment (l). It is defined (Caswell 1989) as the dominant eigenvalue of the projection matrix in the following state-structured but spatially unstructured model,

$$\begin{bmatrix} 0 & 0 & \cdots & & b \\ s & 0 & & & \\ 0 & s & \ddots & & \vdots \\ \vdots & & \ddots & \ddots & \vdots \\ & & & s & 0 & 0 \\ 0 & \cdots & \cdots & 0 & s & s \end{bmatrix} \begin{bmatrix} N_{\tau,0} \\ \vdots \\ \vdots \\ \vdots \\ N_{\tau,l} \end{bmatrix} = \begin{bmatrix} N_{\tau+1,0} \\ \vdots \\ \vdots \\ \vdots \\ N_{\tau+1,l} \end{bmatrix} \quad \text{eqn 7}$$

This definition of λ assumes conditions of indefinite, unrestricted growth. The realized growth rate of the population will, in fact, be lower than the intrinsic growth rate owing to density dependence and the cost of migration.

The possible cost of migration can be manifested either as lower survival or lower fecundity. Survival costs are usually due to predation (Boveng *et al.* 1998). Breeding costs can be due to energetic or social reasons (Danchin & Cam 2002). The metapopulation dynamics may be affected differently depending on whether the penalty for movement is predominantly in survival or in fecundity. We examine the two scenarios separately by implementing the cost of migration as either reduced

fecundity ($0 \leq b' \leq b$) or reduced survival ($0 \leq s' \leq s$). We allow the strength of site fidelity and the cost of migration to vary independently of each other.

We simulate the long-term dynamics of a system of 20 identical colonies under demographic stochasticity only (Caswell 1989). Demographic stochasticity is implemented by making total fecundity a Poisson variate, total survival a binomial variate and migration a multinomial variate. The per capita fecundity and survival probability are provided by a deterministic population model taking account of the strength and type of density dependence and the cost of migration (see below). The migration probabilities are the equilibrium solutions of the transfer model (Appendix I). The values $b = 0.45$, $s = 0.90$ and $l = 5$ are used as the baseline life-history parameters. According to eqn 7 these correspond to an intrinsic population growth rate of 1.1 per annum. The effect of intrinsic growth rate on metapopulation dynamics is examined by increasing it to 1.2 in three ways: first, by changing to $b = 0.95$, then by increasing the survival probability to $s = 0.99$ and finally by reducing the age to recruitment to $l = 2$. Transient dynamics are often as important for the management and conservation of a species as long-term dynamics (Hanski *et al.* 1996; Ovaskainen & Hanski 2002; Hastings 2004). Hence, to observe the entire colonization process, we begin each simulation by seeding one colony with 20 individuals and record the local and global dynamics for the next 300 years.

LOCAL DENSITY DEPENDENCE

High density within the breeding colony is most likely to prevent animals from breeding or increase the mortality of newborns. We therefore implement local density dependence by using a Beverton–Holt term for fecundity as this includes the survival of newborns on the colony:

$$b_{\tau,i} = b \frac{k}{k + N_{\tau,i,l}} \quad \text{eqn 8}$$

The half-saturation parameter k determines the colony population size at which realized fecundity is half of the intrinsic rate b . The values of b and k are assumed to be the same for all colonies and site fidelity is assumed to depend on local density ($N_F > 0$, $r_F = 1$ in eqn 1). In reality, the values of k will always vary between colonies. We do not incorporate such variation because even though it would not influence our conclusions, it would encumber their presentation. Finally, we assume that the breeding colony chosen by prospecting animals is influenced by local density (i.e. $N_S > 0$, in eqn 5) and that they can correctly gauge the realized fecundity of the local population. Because both the density-dependent settling probability (eqn 5) and density-dependent growth (eqn 8) are modelled by the same functional form, this assumption implies that $N_S = k$.

To illustrate the effect of site fidelity on long-term dynamics we examine two extreme scenarios. In one,

the strength of site fidelity is low ($N_F = 10^3$) and in the other it is high ($N_F = 10^6$). In both examples, we use the parameter values $s = 0.9$, $b = 0.95$, $l = 5$ and $k = 50$ and assume that migration is cost-free.

To obtain an overview of the model's behaviour we record the time to complete occupancy in simulations running for up to 300 years for two different values of intrinsic growth rate, and a range of values for the cost of migration on survival and fecundity, and the strength of site fidelity.

Finally, we examine the temporal variability in the colonization process by generating 100 realizations for each of the two extreme examples above. For each of the 300 years, we record mean occupancy and the accompanying 2.5 and 97.5 percentiles from our 100 replicates.

GLOBAL DENSITY DEPENDENCE

Global density dependence may influence the survival of all individuals as well as their fecundity. We therefore implement it by using Beverton–Holt terms for survival and breeding

$$b_\tau = b \frac{K}{K + \sum_{v=1}^l \sum_{j=1}^m N_{\tau,j,v}} \quad \text{and} \quad s_\tau = s \frac{K}{K + \sum_{v=1}^l \sum_{j=1}^m N_{\tau,j,v}} \quad \text{eqn 9}$$

In the absence of local density dependence, colony population size affects neither site fidelity nor the settling probability of migrant animals ($N_F = 0$ in eqn 1 and $N_S = 0$ in eqn 5). The strength of density-independent site fidelity is controlled by the parameter r_F , the proportion of animals that emigrated each year.

Once again we examine two scenarios, using the values $s = 0.9$, $b = 0.95$, $l = 5$, $K = 20000$ with low ($r_F = 0.1$) or high ($r_F = 0.01$) site fidelity. Preliminary results suggest

that the most important summary of the system's behaviour under global density dependence is the variability in local population size. We therefore record the variance-to-mean ratio of local population sizes at the end of 300 years under two different values of the intrinsic growth rate (λ), and a range of values for the cost of migration and the strength of site fidelity. Finally, as in the case of local density dependence, we examine the variability in the colonization process by generating 100 realizations for each of the two scenarios. We record mean occupancy and the accompanying 2.5 and 97.5 percentiles.

Results

SHORT-TERM MOVEMENT MODEL

In the circular colony configuration (Fig. 1a), the distribution of animals is homogeneous after the transfer process is complete. In the linear (Fig. 1b) and random (Fig. 1c) colony configurations, the transfer process gives rise to heterogeneous final distributions. In none of these cases does the final distribution depend on the initial distribution of animals, nor is it affected by site faithful breeders because none exist in these examples. Therefore, the resulting distributions are 'ideal' in the sense that the animals can prospect the entire system of colonies, but they are not 'free' because connectivity limits the rate at which each colony is visited and settled (Fretwell & Lucas 1970; Sutherland 1983).

LONG-TERM METAPOPULATION DYNAMICS

When site fidelity is low, irrespective of the mechanism of population regulation, individual colonies are settled quickly, the aggregate population time series follows a logistic trajectory and complete occupancy of

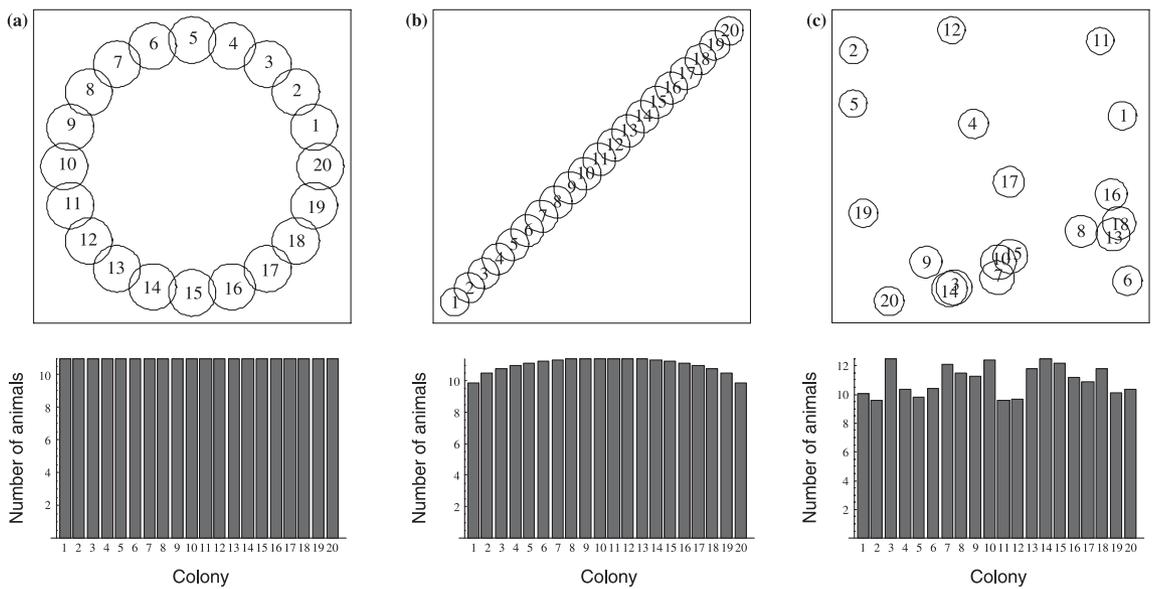


Fig. 1. Equilibrium solutions of the annual movement model for (a) circular, (b) linear and (c) random spatial arrangements of 20 colonies. The top row shows the positions of the colonies in space. The number of animals in each colony at equilibrium are represented by the size of the circles and the histogram in the bottom row.

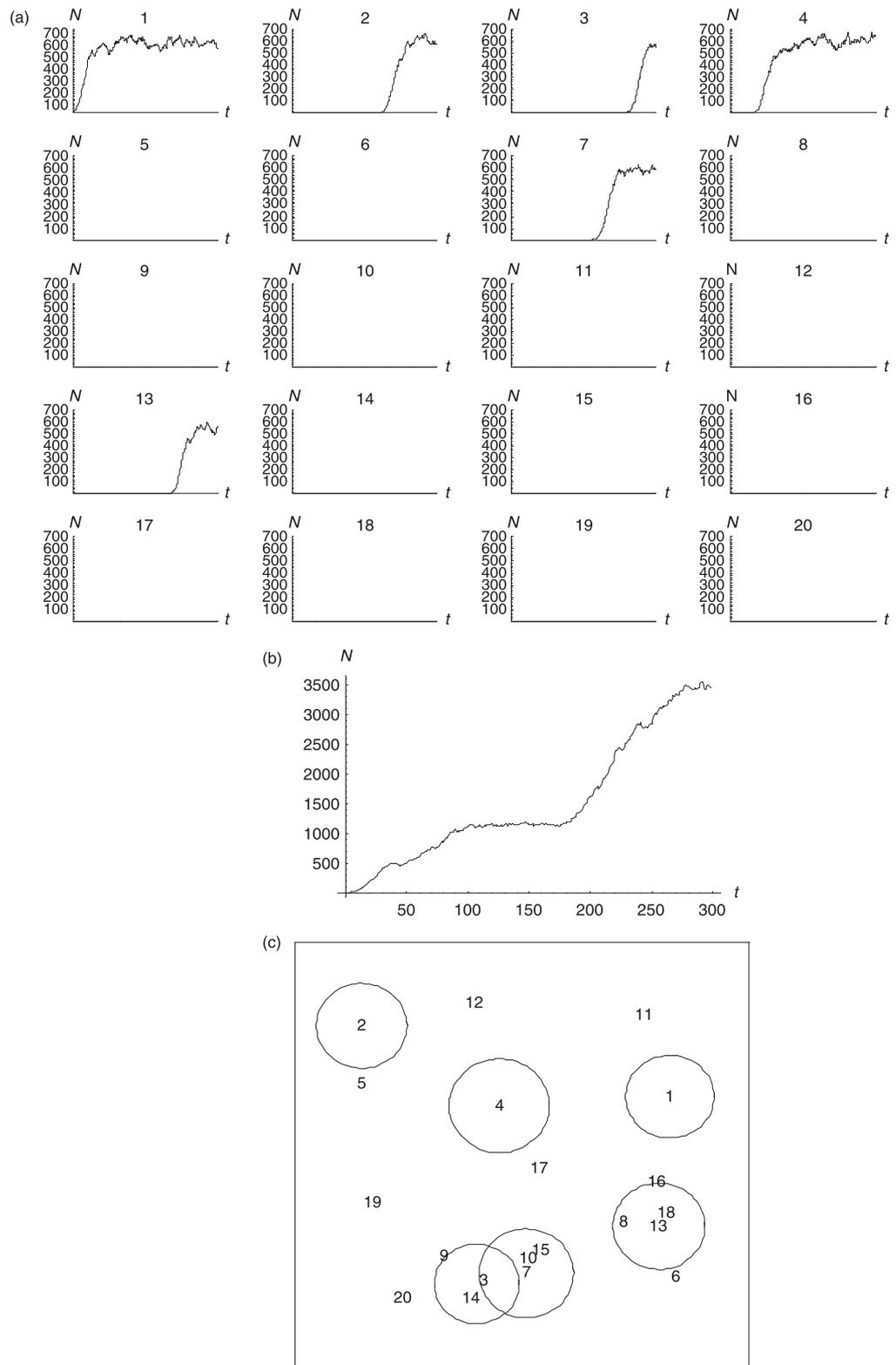


Fig. 2. Individual colony trajectories (a), metapopulation trajectory (b) and spatial view of the metapopulation (c) after 300 years of simulation subject to local density dependence ($k = 50$) and strong site fidelity ($N_F = 10^6$). Emigrants incurred no cost.

the network is quickly achieved. However, with strong site fidelity the metapopulation dynamics depend on the mechanism of population regulation. Under local density dependence there are long time intervals between colonization events (Fig. 2a), the aggregate population

time-series shows multiple plateaus (Fig. 2b) and the colonization process shows no obvious spatial pattern (Fig. 2c). Strong site fidelity keeps animals in their colonies, hence increasing local density and resulting in density-dependent reductions in fecundity. If site

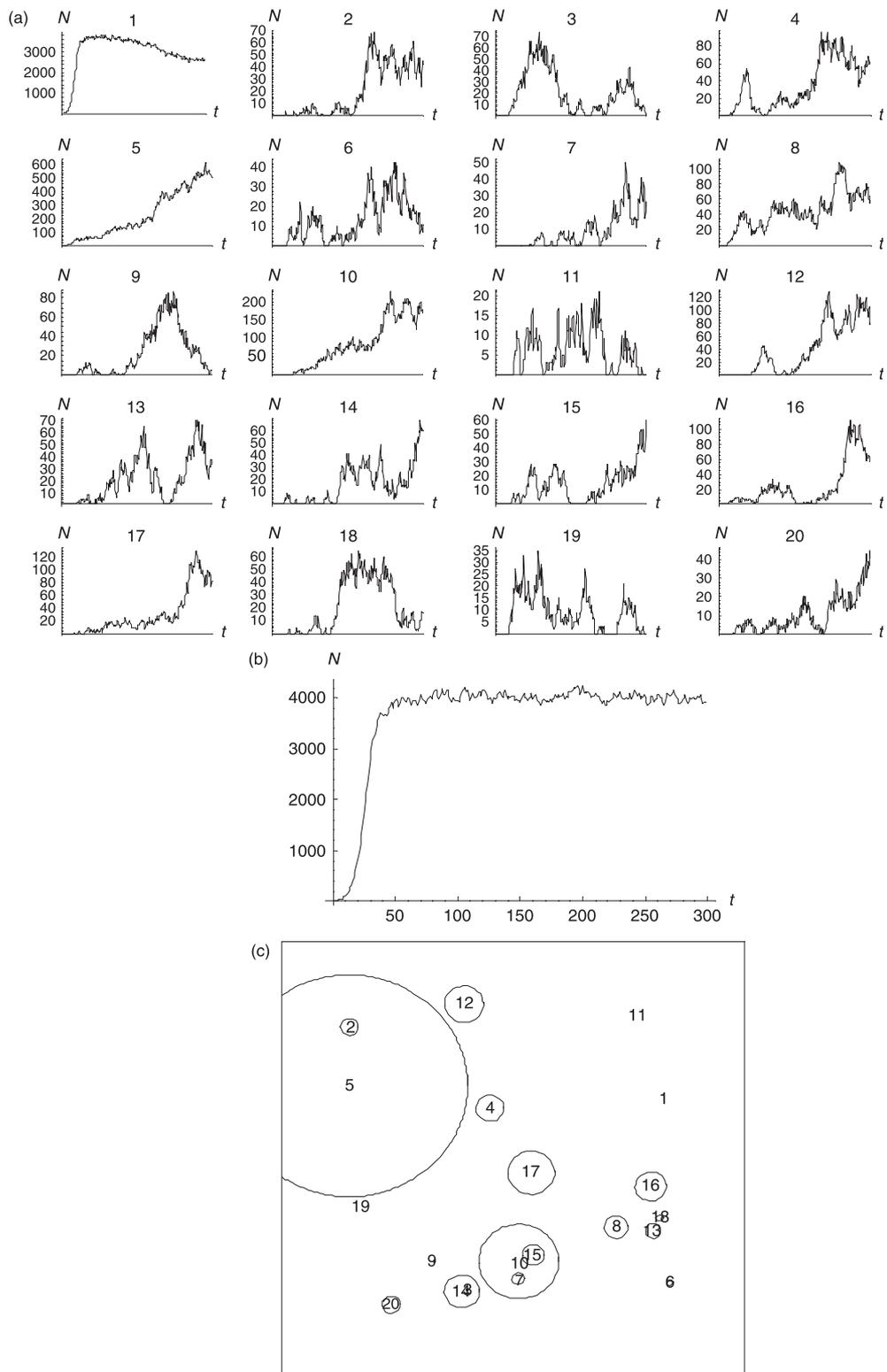


Fig. 3. Individual colony trajectories (a), metapopulation trajectory (b) and spatial view of the metapopulation (c) after 300 years of simulation subject to global density dependence ($K = 20000$) and strong site fidelity ($r_F = 0.01$). A large circle for colony 1 in (c) is not visible.

fidelity is strong enough, fecundity is suppressed to such an extent that there is almost no density-dependent emigration. As a result, the metapopulation becomes trapped in a subset of the available colonies and the aggregate population trajectory displays a plateau until

random, demographic events lead to the production of emigrants.

The combination of global density dependence and strong site fidelity increases variability in the size of each colony (Fig. 3a,c), and leads occasionally to local

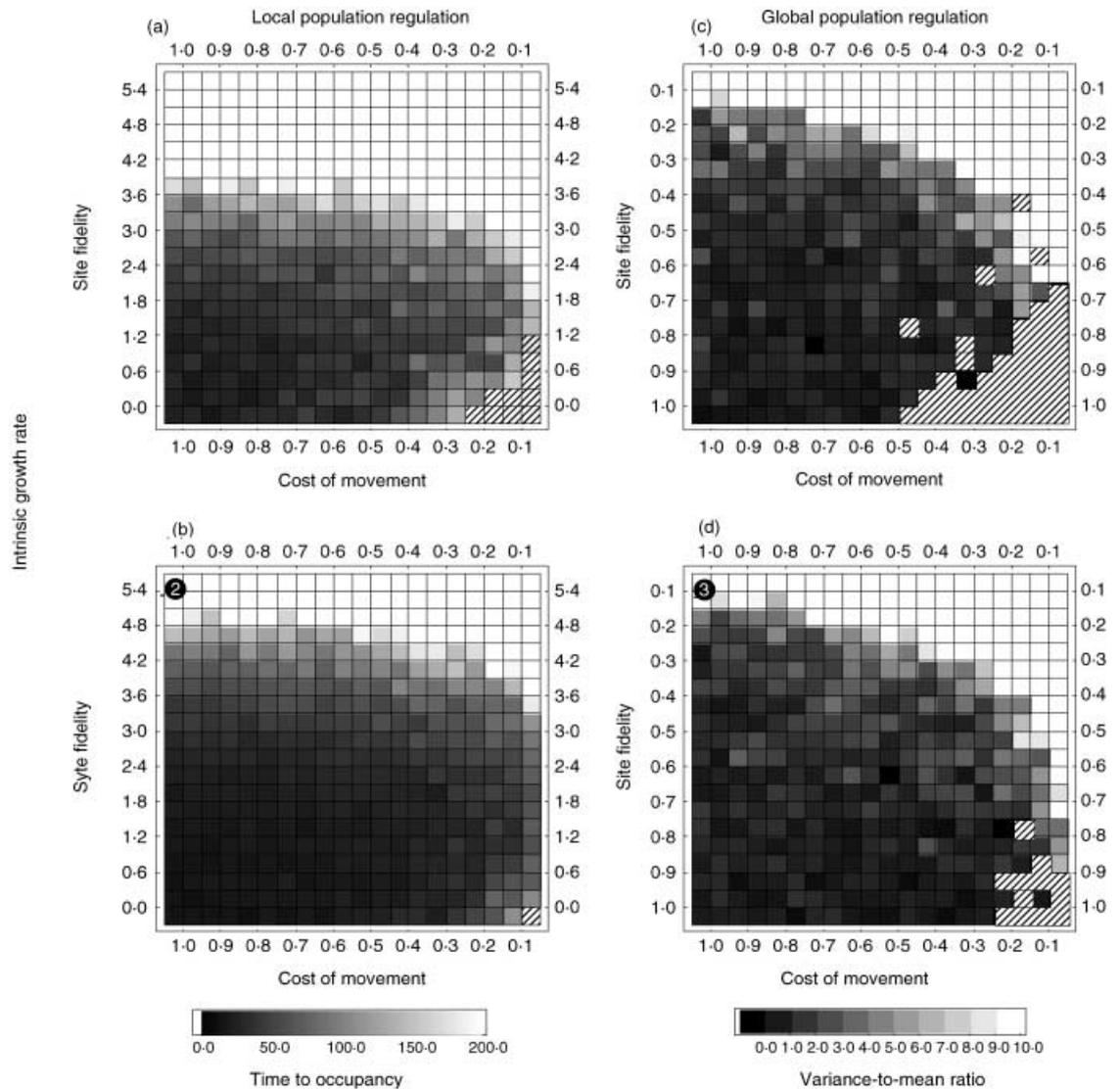


Fig. 4. Occupancy patterns under local and global density dependence, high and low intrinsic growth rate and different values for the strength of natal site fidelity and the cost of movement. Under local density dependence we measured the time taken to achieve complete occupancy. Strength of site fidelity was given by $\log(N_F)$ ranging from 0 (weak) to 6 (strong). Cost of migration was given by the ratio s'/s ranging from 1 (low) to 0 (high). Under global density dependence, we measured variability in colony size as the variance-to-mean ratio of colony population numbers. In this case the strength of natal site fidelity was given by r_F ranging from 1 (weak) to 0 (strong). Hatched regions indicate metapopulation extinctions. The parameters used for the simulations in Figs 2 and 3 correspond to the points marked (2) and (3).

extinctions. The aggregate trajectory for the metapopulation (Fig. 3b) does not reflect this variability in local population sizes. Strong site fidelity leads to competition between colonies for the shared, limiting resource. Colonies that gain an advantage by being occupied early are less vulnerable to extinction through demographic stochasticity. Their growth indirectly suppresses the growth in other colonies making them more susceptible to chance, demographic events and extinction.

Incorporating a migration cost in the form of reduced fecundity has no impact on the patterns of occupancy because this merely results in a temporary postponement in breeding for migrating individuals. Once they have settled, they can breed and found the new colony in the next year. This is significant because, at least for

birds, migration costs are more likely to impact on fecundity and therefore have no effect on the colonization process.

On the other hand, incorporating a cost of movement as reduced survival has considerable impact on occupancy patterns. Under local density dependence, increasing the cost of migration and the strength of site fidelity tends to delay full occupancy (Fig. 4a). Under global density dependence, increasing the cost of migration and the strength of site fidelity increases the variability in colony size (Fig. 4b). In both cases, low site fidelity combined with a high cost of migration reduces the population's growth rate because more individuals leave their colonies and pay a high price for doing so. This sometimes leads to global extinction. In general, a high cost of movement impedes the

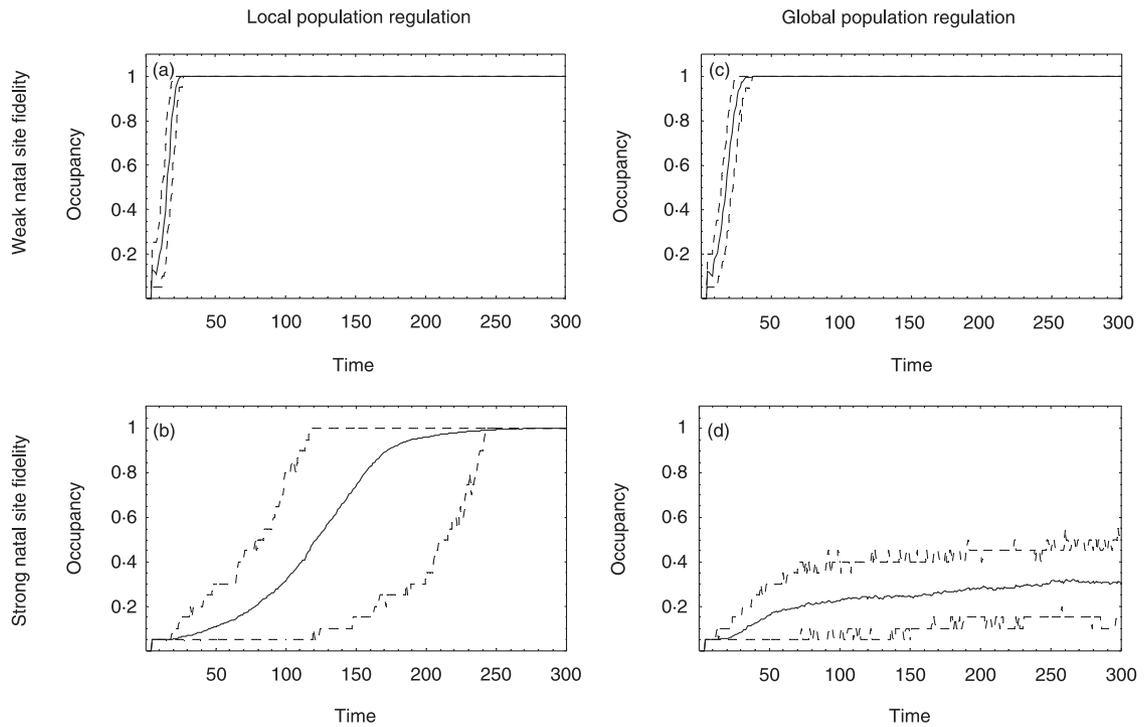


Fig. 5. Mean occupancy as a function of time, and the accompanying 2.5 and 97.5 percentiles obtained from 100 realizations of each simulation ($s = 0.9$, $b = 0.95$, $l = 5$). Under local population regulation we used $k = 50$, $N_F = 10^2$ (weak fidelity) and $N_F = 10^6$ (strong fidelity). Under global population regulation we used $K = 20000$, $r_F = 0.1$ (weak fidelity) and $r_F = 0.001$ (strong fidelity).

free exchange of individuals between existing and potential colonies and hence increases both the time to complete occupancy and the variability in colony size. These patterns are consistent for different values of λ (Fig. 4c,d) but, as might be expected, the average time to complete occupancy and the risk of global extinction decreases with increasing values of λ . The effects of increased growth rate do not depend on how the increase is achieved (i.e. by increasing survival, increasing fecundity or decreasing the age to recruitment).

Finally, the transition from an unoccupied to a fully occupied colony network is characterized by a larger degree of variability when there is strong site fidelity and local density dependence (Fig. 5), because colonization events are primarily a consequence of demographic stochasticity. Under global density dependence the proportion of occupied colonies is also more variable under strong site fidelity and complete occupancy is prevented altogether when site fidelity is very strong. This is not a transient phenomenon: allowing our simulations to run for another 900 years does not result in increased occupancy.

Discussion

We believe that these simulations capture the essential features of the population dynamics of a large class of animals that conform to the metapopulation paradigm for only part of their life histories. To examine the metapopulation's short-term dynamics, we developed a biologically plausible model of movement between breeding colonies and used it to derive an equilibrium

redistribution function. The resulting spatial distribution is 'ideal' but not 'free' (Fig. 1). These are desirable properties of a transfer model for colonially breeding mammals and birds because, even though individuals have the mobility and time to sample many colonies, the annual redistribution is still subject to the restrictions imposed by colony connectivity.

The equilibrium assumption used to derive the redistribution function is supported by theoretical (Boulinier & Danchin 1997; Schjørring 2002) and empirical (Halley & Harris 1993; Halley, Harris & Wanless 1995; Bradley *et al.* 1999; Schjørring, Gregersen & Bregnballe 1999) evidence that individuals spend the years prior to breeding prospecting for suitable colonies. It is not essential for the transfer model but it does result in considerable computational economy. Such time-saving devices are needed if annual movement models are to be incorporated in population models whose parameters are estimated using computer-intensive statistical algorithms, such as Markov chain Monte Carlo (O'Hara *et al.* 2002; Drechsler *et al.* 2003) or sequential importance sampling (Buckland *et al.* 2004).

In order to write our transfer model as a set of balance differential equations, we made the assumption that there is no change in total population size while the animals are redistributing. This assumption will be true even if migration affects fecundity, but it will only be approximately true if migration affects survival. Problems with the validity of this assumption may be aggravated by the biological mechanism underlying the cost of migration. If the cost of migration is sublethal (e.g.

due to energetic or social factors), then it will impact primarily on fecundity, following the completion of migration, as assumed here. If, on the other hand, it is due to death (e.g. predation) occurring during migration, then our assumption of no population change will be incorrect.

Our investigation of long-term dynamics focused on the behavioural trade-off between migration and site-fidelity, and the demographic trade-off between intrinsic growth and population regulation. This enabled us to explore the global and local dynamics of a spatially explicit metapopulation model, over a large portion of the parameter space. To do this we had to ignore factors such as the interaction between carrying capacity and demographic stochasticity, and the effect of environmental stochasticity. These processes can operate in a bewildering variety of ways, and we believe that their effects would be better studied using information from specific biological systems.

Our results suggest that strong site fidelity delays or prevents full occupancy of a colony network, and help to explain observed heterogeneities in the distribution of colonially breeding species that do not appear to be the result of a lack of suitable colony sites (e.g. Furness & Birkhead 1984). Despite the movement capabilities of most colonial breeders, it would be a mistake to interpret colony occupancy as identical to colony suitability.

Site-fidelity effectively increases the isolation between colonies, so some of the results presented here might have been derived from classical metapopulation models, parameterized for low connectivity. However, when reductions in connectivity result from site fidelity, new colonizations will be only weakly spatially correlated with the source populations (Figs 2c and 3c). This is because, in colonial breeders, the rarity of colonization events is primarily a result of the reluctance of individuals to leave their natal colony rather than the distance between colonies.

Other mechanisms leading to aggregations of conspecifics, such as the Allee effect (Courchamp, Clutton-Brock, & Grenfell 1999; Oro & Ruxton 2001), could give rise to similar metapopulation dynamics. Indeed, our conclusions are in agreement with previous theoretical studies (Amarasekare 1998; Gyllenberg, Hemminki, & Tammaru 1999) of the Allee effect in two-patch metapopulations. Like us, these studies found that conspecific aggregation can give rise to heterogeneity in metapopulations, lead to reductions in the metapopulation growth rate and prevent an increase in the metapopulation, even with abundant habitat and positive projected growth.

We demonstrated that, depending on the strength of site fidelity, markedly different types of population dynamics and patterns of colonization occur when density dependence is local or global. Under strong site fidelity, local density dependence eventually leads to complete occupancy whereas global density dependence prevents it. In theory, this qualitative feature of the dynamics could be used to diagnose the type of density dependence regulating a population. However, this is unlikely to be a useful practical diagnostic for three

reasons. First, most real population time-series are relatively short, compared to the time scales discussed in this paper. Secondly, patterns of occupancy will be confounded by environmental stochasticity especially if it is strong enough to cause local, catastrophic extinctions (Dennis 2002). Thirdly, it is possible that local and global population regulation operate simultaneously (Frederiksen, Lebreton & Bregnballe 2001) or alternatively, thus keeping the population in a state of transient dynamics.

We allowed site fidelity and the cost of movement to vary independently of each other. In reality, they will be linked by evolution (Hamilton & May 1977; Johnson & Gaines 1990; Heino & Hanski 2001; Cadet *et al.* 2003). However, it is well known that site fidelity can be maladaptive, particularly if the mechanism and spatial scale of population regulation varies with time (Cooch *et al.* 1993; Renken & Smith 1995; Ganter & Cooke 1998; Spear *et al.* 1998). Hence, rather than examining only some evolutionarily stable relationship between the strength of site fidelity and the cost of migration, we opted for this more general approach.

Our work underlines the importance of individual behaviour for population dynamics and has implications for conservation and management. Under local density dependence, site fidelity prolongs the time taken for the metapopulation to reach carrying capacity. It therefore reduces the apparent growth rate of the metapopulation and causes a discrepancy between local and global population growth rates. If site fidelity is strong enough, the environment is only mildly stochastic and the population time series extends far enough into the past, then the occurrence of multiple plateaus (Fig. 2b) will alert us to the cause of this discrepancy. However, projections of metapopulation growth based on local growth rates (Lalas & Bradshaw 2003) may be over-optimistic if site fidelity is only moderately strong (Coulson & Demevergnies 1992), if its effect is clouded by environmental stochasticity, or if the available time-series is short.

There is evidence that the transient plateaus in metapopulation time-series predicted by our model also occur in the wild (Frederiksen *et al.* 2004 – compare their Fig. 1 with our Fig. 2b). Each of these may be interpreted incorrectly as the environment's carrying capacity. A management strategy based on this interpretation could have unexpected outcomes. For example, attempts to control a pest population by reducing the number of established colonies, rather than the number of potential colonies, may precipitate dispersal of previously site-faithful animals and lead to an increase in metapopulation size.

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Appendix I

FINDING THE EQUILIBRIUM SOLUTIONS OF THE ANNUAL TRANSFER MODEL

At equilibrium, we introduce the new variable

$$x_i = P_{\tau,i}^* g(M_{\tau,i} + P_{\tau,i}^*), \quad \text{eqn A1}$$

The steady-state solutions of eqn 6 are now given by the linear system

$$(\mathbf{h} - \mathbf{I})\mathbf{x} = \mathbf{0} \quad \text{eqn A2}$$

where \mathbf{h} is the matrix of jump probabilities in eqn A2 and \mathbf{I} is the $m \times m$ identity matrix. The column elements of the matrix $\mathbf{h} - \mathbf{I}$ add up to zero eqn A4, which means that the system in (A2) has one less equations than unknowns. This is a consequence of the assumption that no deaths or births occur during migration. Therefore, we seek to solve (A2) under the constraint

$$\sum_{i=1}^m P_{\tau,i}^* = \sum_{i=1}^m P_{\tau,i}(0) \quad \text{eqn A3}$$

The system in eqn A3 is solved for all but the last equation to get m^{-1} expressions of the type

$$x_i = H_i x_m \quad \text{eqn A4.}$$

Assuming that (A1) can be inverted we write it as

$$P_{\tau,i}^* = q(x_i) \quad \text{eqn A5}$$

Combining eqns A3–A5 the problem is reduced to finding the solution of $\sum_{i=1}^m q(H_i x_m) = \sum_{i=1}^m P_{\tau,i}(0)$. This is a single algebraic equation in x_m . In the example of eqn 5, the variable x_i is written $x_i = (M_{\tau,i} + P_{\tau,i}^*) P_{\tau,i}^* / (N_S + M_{\tau,i} + P_{\tau,i}^*)$. This has only one positive solution, $P_{\tau,i}^* = \frac{1}{2}(x_i - M_{\tau,i} + \sqrt{(x_i + M_{\tau,i})^2 + 4N_S x_i})$ which yields the equation

$$\sum_{i=1}^m \frac{H_i x_m - M_{\tau,i} + \sqrt{(H_i x_m + M_{\tau,i})^2 + 4N_S H_i x_m}}{2} = \sum_{i=1}^m P_{\tau,i}(0) \quad \text{eqn A6}$$

This equation has no closed-form solution, but is readily solved numerically.