Metapopulation models are widely used to study species that occupy patchily distributed habitat, but are rarely applied to migratory species, because of the difficulty of identifying demographically independent subpopulations. Here, we extend metapopulation theory to describe the directed seasonal movement of migratory populations between two sets of habitat patches, breeding and non-breeding, with potentially different colonization and extinction rates between patch types. By extending the classic metapopulation model, we show that migratory metapopulations will persist if the product of the two colonization rates exceeds the product of extinction rates. Further, we develop a spatially realistic migratory metapopulation model and derive a landscape metric—the migratory metapopulation capacity—that determines persistence. This new extension to metapopulation theory introduces an important tool for the management and conservation of migratory species and may also be applicable to model the dynamics of two host–parasite systems.

Keywords: seasonal migration; metapopulation; migratory network

1. INTRODUCTION

The term metapopulation, coined by Levins [1], is used to describe a population comprising many spatially discrete subpopulations connected by dispersal [1,2]. The metapopulation concept includes any system in which subpopulations inhabit discrete habitat patches and interpatch dispersal is both high enough to ensure demographic connectivity among patches yet low enough to maintain some degree of independence in local population dynamics [2].

The simplest metapopulation model, the Levins model [1,3], yields the result that the proportion of habitat patches occupied depends on the ratio of colonization and extinction rates, and the former must exceed the latter for metapopulation persistence. An extension of metapopulation theory, ‘spatially realistic metapopulation theory’ [4,5], describes a system with a finite set of patches, variation in patch qualities and variation in patch isolation resulting from distance-dependent migration. These models do not describe the local population dynamics but only the likelihood of patch occupancy. The extensive development of all branches of metapopulation theory has largely been driven by conservation applications, and many taxa have been successfully described using a metapopulation approach [2].

Despite its usefulness, metapopulation theory has rarely been applied to migratory species, i.e. species that undergo directed seasonal movement between breeding and non-breeding areas [6], a life-history characteristic common among, but not restricted to, avian species. The main obstacle is the difficulty of identifying demographically independent subpopulations in migratory species [7]; individuals occurring in separate subpopulations in the breeding season may not be separated in the non-breeding season, and vice versa. In the few cases in which metapopulation models have been applied to migratory animals, the assumption of a spatially homogeneous non-breeding habitat is implicit [8,9]. When habitat in both seasons is spatially discrete, it becomes difficult to separate a population into demographically independent units, leaving uncertainty as to how, or whether, migratory species fit into the metapopulation concept [10].

The problem can be resolved by considering the system to be a migratory network [11,12], comprised distinct sets of geographically defined, discrete patches: breeding and non-breeding. Two different approaches have been applied to the network framework; a model with connectivity described as time-varying transition functions between patches [11], and an N-population model where connectivity is derived by finding a dynamic population equilibrium [12]. Neither approach, however, allows for colonization or extinction of patches.

Here, we present a novel extension to metapopulation theory, applicable to migratory species. The migratory metapopulation model differs from the classic metapopulation model in having two patch types: breeding and non-breeding, with directed movement between these two types occurring strictly sequentially. Our definitions of occupancy, colonization and extinction also differ for a migratory metapopulation. Here, a patch is occupied if it is used during its relevant season even though it is unused during the rest of the year; it remains occupied if individuals return to it in the following year. Colonization refers to a patch that is unoccupied in the previous year becoming occupied by individuals arriving from patches of the opposite type. Extinction occurs if a site that was occupied in the previous year fails to be reoccupied in the current year. We assume that patches are colonized at the beginning of each season when migrants return, and that patch occupancy does not subsequently change within a season. We show how both the classic metapopulation model [1,2] and the spatially realistic metapopulation model [4,5] can be extended to migratory species.

2. MIGRATORY METAPOPULATION MODEL

The Levins model has one variable, \( p \), the proportion of patches occupied [2]. The dynamics of \( p \) are

\[
\frac{dp}{dt} = cp(1-p) - mp.
\]

(2.1)

where \( c \) and \( m \) are the intrinsic patch colonization and extinction rates. This model has a single, non-trivial equilibrium \( p = 1 - (\mu/c) \), which exists if \( c > \mu \).
To extend this model to migratory species, we assume that in year \( t \) there are a set of breeding patches of which proportion \( p_i \) is occupied (i.e. used during the breeding season) and a distinct set of non-breeding patches of which proportion \( q_j \) is occupied (i.e. used during the non-breeding season). Colonization depends on the previous year’s proportions of seasonally unoccupied patches of the same type, and seasonally occupied patches of opposite type. Extinction, or failure to seasonally reoccupy previously occupied patches, depends on the proportion of seasonally occupied patches of the same type last year. Most patches’ occupancy status does not change between years. We describe these dynamics using a discrete-time model. The proportions of occupied patches in year \( t + 1 \) are

\[
\begin{align*}
    p_{t+1} &= p_t + c_B q_t (1 - p_t) - \mu_B p_t \\
    q_{t+1} &= q_t + c_W p_t (1 - q_t) - \mu_W q_t,
\end{align*}
\]  
(2.2)

where \( c_B \) and \( \mu_B \) are the intrinsic colonization and extinction rates of breeding patches; \( c_W \) and \( \mu_W \) are the analogous rates for non-breeding patches (all take values from 0 to 1 to ensure that \( p_t \) and \( q_t \) also remain bounded). We solve for the long-term equilibria proportions of occupied patches (electronic supplementary material), which are extinction \( (p = \dot{q} = 0) \) and persistence

\[
\dot{p} = \frac{c_B c_W - \mu_B \mu_W}{c_B (c_B + \mu_B)} \quad \text{and} \quad \dot{q} = \frac{c_W c_B - \mu_W \mu_B}{c_W (c_W + \mu_W)}.
\]  
(2.3)

Both \( \dot{p} \) and \( \dot{q} \) depend on colonization and extinction rates in both seasons and the condition for persistence is \( c_B c_W > \mu_B \mu_W \).

Sensitivity to changes in colonization and extinction rates—calculated by differentiating \( \dot{p} \) and \( \dot{q} \) with respect to \( c \) and \( \mu \)—shows that occupancy in both seasons increases as colonization rates increase and decrease as extinction rates increase. Thus, extinction and colonization rates at non-breeding sites affect the proportion of breeding patches occupied and vice versa. However, equilibrium occupancy of each patch type is generally more affected by changes in the rates in that season than in the alternate season (figure 1).

### 3. SPATIALLY REALISTIC MIGRATORY METAPOPULATION MODEL

In a spatially realistic metapopulation model [4,5], each patch \( i \) has an area \( A_i \) and a location. The occupancy probability of patch \( i \) is given by \( p_i \) and \( \dot{p} \) is the vector of all \( p_i \). The model dynamics are

\[
\frac{dp_i}{dt} = C_i(\dot{p}) (1 - p_i) - E_i p_i.
\]  
(3.1)

Colonization of patch \( i \) is possible from every other patch \( j \) and depends on the area of the source patch \( A_j \), its occupancy probability \( p_j \) and the interpatch distance \( d_{ij} \), yielding a colonization rate \( C_i(\dot{p}) = c \sum_j A_j A_i e^{-\alpha d_{ij}} \). The parameter \( \alpha \) is 1/the average migration distance of the species. Smaller patches experience higher extinction rates, yielding the patch extinction rate \( E_i = \mu / A_i \). The metapopulation persists if \( \lambda_M > \delta \), where \( \delta = \mu / c \) and \( \lambda_M \), called the metapopulation capacity, is the leading eigenvalue of a landscape or metapopulation matrix \( M \) [4,5].

\[
\begin{align*}
    p_i(t + 1) &= p_i(t) + c_B N_{WB} \sum_{j=N_B+1}^{N_B+N_W} q_j(t) A_j \dot{p} e^{-\alpha d_{ij}} (1-p_i(t)) \\
    &\quad - \frac{\mu_B}{A_i} p_i(t) \tag{3.2}
\end{align*}
\]  

and

\[
\begin{align*}
    q_j(t + 1) &= q_j(t) + c_W N_B \sum_{i=1}^{N_B} p_i(t) A_i \dot{q} e^{-\alpha d_{ij}} (1-q_j(t)) \\
    &\quad - \frac{\mu_W}{A_i} q_j(t), \tag{3.3}
\end{align*}
\]
migrations between breeding and non-breeding areas. Other metapopulation models with multiple patch types demonstrate single-species metapopulation persistence through successional processes [13] or multi-species persistence through differences in patch quality [14]. This is the first work examining how migratory metapopulation persistence depends on seasonal colonization and extinction rates of both breeding and non-breeding patches. This highlights the management importance of measuring colonization and extinction rates for both patch types; measuring these rates at breeding sites only may overestimate metapopulation persistence if non-breeding sites have low colonization and/or high extinction rates. Conversely, one season may act as a buffer against metapopulation extinction when the ratio of colonization : extinction rates is low in the opposite season.

One of the most useful findings of spatially realistic metapopulation theory is that persistence occurs when \( \lambda_M \) a metric that depends only on the landscape characteristics, exceeds a threshold value that depends only on species characteristics [4,5]. \( \lambda_M \) has been used to predict the relative likelihood of persistence in different landscape configurations [4,15], the consequences of habitat loss [16,17], and extinction risk and extinction debts in fragmented landscapes [16]. We have derived an analogous metric (\( \lambda_{MM} \)) for migratory species with the same potential utility that \( \lambda_M \) has for non-migratory species.

The spatially realistic migratory metapopulation model assumes that extinction rates will be negatively related to patch size, and some colonially breeding, migratory birds have been shown to meet this assumption [9,18]. However, unlike non-migratory metapopulations, the migratory model assumes that colonization occurs when individuals return from the opposite season and therefore predicts that colonization rates should be related to isolation from patches in the opposite season rather than in same season. This appears never to have been tested for any migratory animals. Colonization rates of breeding patches are sometimes related to isolation from other breeding patches [9,18] and this is used as evidence that colonists are colonizing from other breeding patches. However, this finding could also be explained by noticing that breeding patches isolated from other breeding patches may also be more isolated from non-breeding patches. It should also be noted that, as in other metapopulation applications, distance may not be strictly geographical distance but could incorporate measures of the cost of movement between the two sites.

The models described are appropriate for species that undertake to and fro migrations [6] between two stages. For these models to apply, the species must occupy patchily distributed habitat in both stages and the habitat patches must be described at a spatial scale at which occupancy changes are observed annually. For several birds, surveys of breeding habitat show year-to-year changes in patch occupancy [7] and, although less is often known about the non-breeding season, it seems reasonable to assume that non-breeding habitat is also patchily distributed. Our approach could be extended to model migratory systems with multiple stages (e.g. breeding, staging and over-wintering), or to use more realistic measures of patch connectivity and quality than

\[
A_1 = 1 \\
A_2 = 2 \\
A_3 = 2 \\
A_4 = 1 \\
d_{14} = \text{variable} \\
d_{13} = 1 \\
d_{23} = \text{variable} \\
d_{24} = 1 \\
\]

where colonization and extinction rates are positive and bounded above to ensure occupancy probabilities lie in [0,1]. Using the techniques in the study of Ovaskainen & Hanski [5], we show that the migratory metapopulation persists if \( \delta_{MM} > \sqrt{\delta_B \delta_W} \), where \( \delta_B = (\mu_B / c_B) \) and \( \delta_W = (\mu_W / c_W) \) is the leading eigenvalue of the migratory metapopulation landscape matrix (figure 2). This matrix is similar to the matrix for the non-migratory model, except the elements are zero if both source and destination are breeding patches or if they are both non-breeding patches (electronic supplementary material).

4. DISCUSSION

We have extended single-species metapopulation theory to describe animals undergoing strictly sequential
interpatch distance and patch area (e.g. allowing patch quality to vary with spatial location and between years). However, our framework is not applicable to some migration strategies, such as the multi-generational migration of monarch butterflies (Danaus plexippus [6]).

The two-patch type model might be applicable to the transmission dynamics of parasites with two obligate hosts, such as the trematode, Schistosoma mansoni, the agent of the disease schistosomiasis. The schistosome life cycle includes a definitive host (i.e. human) where the parasite reproduces sexually, and a snail host where several asexual reproductive stages occur. Application of the two-patch type model to this system would assume that transmission (colonization) of each host type depends on infection prevalence in the alternate host.

This work is funded by NSF Award DEB-0933602 (PI:T aylor).