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Modeling Seasonal Interactions in the Population Dynamics of Migratory Birds

U NDERSTANDING THE POPULATION DYNAMICS of migratory birds requires understanding the relevant biological events that occur during breeding, migratory, and overwintering periods. The few available population models for passerine birds focus on breeding-season events, disregard or oversimplify events during nonbreeding periods, and ignore interactions that occur between periods of the annual cycle. Identifying and explicitly incorporating seasonal interactions into population models for migratory birds could provide important insights about when population limitation actually occurs in the annual cycle. We present a population model for the annual cycle of a migratory bird, based on the American Redstart (*Setophaga ruticilla*) but more generally applicable, that examines the importance of seasonal interactions by incorporating: (1) density dependence during the breeding and winter seasons, (2) a carry-over effect of winter habitat on breeding-season productivity, and (3) the effects of behavioral dominance on seasonal and habitat-specific demographic rates. First, we show that habitat availability on both the wintering and breeding grounds can strongly affect equilibrium population size and sex ratio. Second, sex ratio dynamics, as mediated by behavioral dominance, can affect all other aspects of population dynamics. Third, carry-over effects can be strong, especially when winter events are limiting. These results suggest that understanding the population dynamics of migratory birds may require more consideration of the seasonal interactions induced by carry-over effects and density dependence in multiple seasons. This model provides a framework in which to explore more fully these seasonal dynamics and a context for estimation of life history parameters.

INTRODUCTION

The factors that limit and the mechanisms that regulate the dynamics of bird populations are often poorly understood (Murdoch 1994; Sutherland 1996; Rodenhouse et al. 1997; Rodenhouse et al. 2003; Sillett and Holmes, Chap. 32, this volume), especially for migratory birds. Identifying the factors driving the population dynamics of migratory birds requires understanding the relevant biological events that occur during breeding, migration and overwintering periods. Available population models for migratory passerine birds tend to focus on breeding-season events, oversimplify events during nonbreeding periods, and ignore interactions that occur between periods of the annual cycle. Models that identify relevant events in the nonbreeding season and explicitly incorporate how different periods of the annual cycle interact could provide a more accurate picture of population dynamics than models that omit these dynamics. In addition, such models may provide important insights about when in the annual cycle limitation occurs.

Despite considerable effort to study the factors that limit migratory bird populations, our understanding of when and how these populations are limited remains poor (Marra and Holmes 2001; Sillett and Holmes 2002; Rodenhouse et al. 2003). Until recently, the prevailing view was that migratory bird populations were limited primarily by events on their wintering grounds (e.g., Fretwell 1972; Alerstam and Högstedt 1982; Robbins et al. 1989; Baillie and Peach 1992; Rappole and MacDonald 1994). Support for this hypothesis comes mainly from evidence such as population declines associated with weather extremes in winter and declines correlated with winter-habitat loss. Alternative hypotheses include: (1) summer limitation, perhaps due to high nest predation and parasitism at high densities (e.g.,

Holmes et al. 1986; Sherry and Holmes 1992; Böhning-Gaese et al. 1993), with evidence seen in correlations between local reproductive success and changes in local breeding populations; and (2) simultaneous summer and winter limitation (Sherry and Holmes 1995).

Results of recent research suggest that while the summer-limitation, winter-limitation, and summer-and-winter limitation hypotheses have some empirical support, they are likely overly simplistic (Marra et al. 1998; Marra and Holmes 2001; Sillett and Holmes 2002; Webster and Marra, Chap. 16, this volume). Periods of the annual cycle appear to be linked inextricably, such that ecological circumstances within one season subsequently influence reproductive success and/or survival in a subsequent season, effects we term "seasonal interactions" (fig. 28.1). We propose two general mechanisms by which there might be ecological interactions between the seasons of the annual cycle: at the *individual* or *population* levels.

The essence of seasonal interactions at the individual level is that individuals carry over effects, such as poor physical condition or late arrival, from one season to the next, and that these residual effects explain ecologically relevant variation in demographic rates in a later season. In contrast, seasonal interactions at the population level occur when the size of the population "carries over" the seasonal effect and is driven by density-dependent processes in each season. For example, an increase in population size leaving the winter grounds leads to higher densities, hence lower reproductive success, in the following breeding season. Theoretically, carry-over effects can influence density-dependent effects, and both individual- and population-level seasonal interactions simultaneously influence population dynamics.

Evidence is mounting for the importance of seasonal interactions at the individual level via carry-over effects. For example, poor physical condition during one season may ex-

Fig. 28.1. A schematic for seasonal-interaction mechanisms in the population dynamics of a Neotropical migratory bird. Migrants occupy habitats ranging in quality, which influences physical condition and winter departure times. These carry-over effects (which are an individually based seasonal interaction) can subsequently influence reproductive success on the breeding grounds. The mechanism for population-level seasonal interaction is via density-dependent survival and reproductive processes on the winter and breeding grounds.
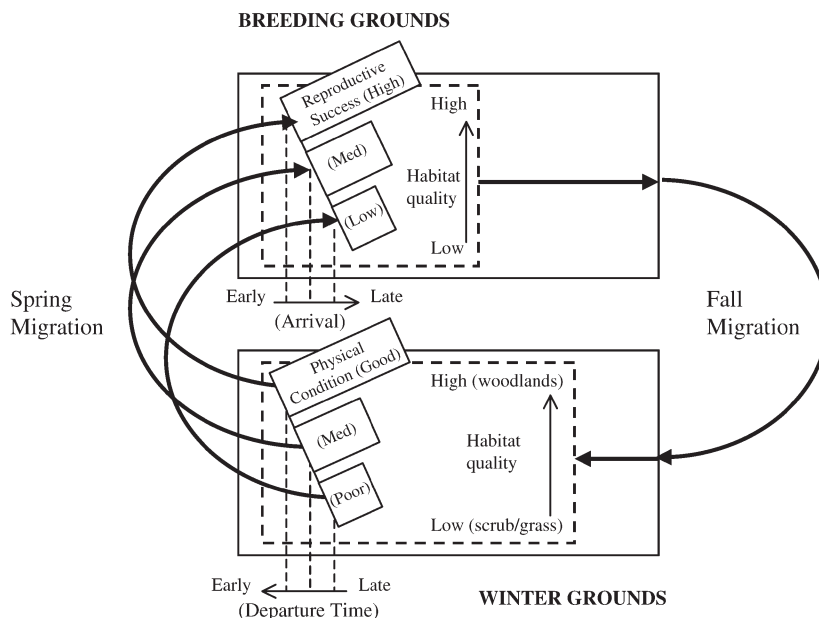
plain variation in reproductive success or survival in a subsequent season. Research on waterfowl initially supported this idea when it was discovered that good environmental conditions on the wintering grounds correlated with higher recruitment the following summer (Heitmeyer and Fredrickson 1981; Kaminski and Gluesing 1987). More recently, Marra et al. (1998) have shown that winter habitat influences the timing of spring migration and the physical condition of American Redstarts (*Setophaga ruticilla*) at time of departure, which in turn influences arrival time and body condition on breeding grounds and ultimately reproductive success (Norris et al. 2004). By affecting the timing of arrival on breeding grounds, carry-over effects could influence access to high-quality territories and the number of possible breeding attempts. Changes in the timing of and physical condition upon arrival are both mechanisms by which effects from the wintering grounds and/or migration period can persist into the breeding season.

Little evidence supports the importance of seasonal interactions at the population level, but this is likely a demonstration of the difficulty of obtaining such data, rather than testimony against such interactions. Direct evidence that seasonal interactions affect population processes would be provided, for instance, by observing a smaller decline in breeding density than expected from a known loss of winter habitat, which would suggest that density-dependent processes in a later season compensated for the loss of habitat. Such evidence is extremely difficult to obtain, because the corresponding winter and breeding ranges and demography are very rarely known and even less often successfully monitored. The oft-debated evidence for compensatory harvest mortality in ducks (Anderson and Burnham 1976) and the oystercatcher work of Goss-Custard et al. (1995c, 1995d) are both cases where such interactions are suggested. There is also some tantalizing evidence for another mode of seasonal interaction, namely, a single external process acting on more than one season: Sillett et al. (2000) found that both breeding- and winter-season dynamics of Black-throated Blue Warblers (*Dendroica caerulescens*) were affected by climatic variation associated with the El Niño Southern Oscillation.

Few attempts have been made to develop a year-round population model for a migratory bird that explicitly incorporates winter and breeding-season events. Sutherland and Dolman (1994) present a population model for a migratory bird that demonstrates how equilibrium population size depends on how individuals interact and compete year-round. Such interactions result in density-dependent interference competition, resource depletion, and, ultimately, mortality. Further work by Sutherland (1996, 1998) has generally concluded that equilibrium population size for a migratory bird species is determined by the relative strengths of density dependence operating during both the breeding and nonbreeding seasons. These models incorporate population-level seasonal interactions but do not consider individual-level carry-over effects or distinguish between the sexes.

To understand better the significance of individual- and population-level seasonal interactions, we developed an empirical model for a migratory songbird that experiences density dependence on the breeding and winter grounds, shows behavioral dominance, and can carry individual effects over from winter to summer. The development of this model relies heavily on insights from our studies of the American Redstart. On their breeding grounds, redstarts show strong age-specific habitat segregation (Ficken and Ficken 1967; Sherry and Holmes 1997) driven by dominance behavior of older males (Sherry and Holmes 1989). In addition, redstarts exhibit strong territorial behavior (Holmes et al. 1989; Ornat and Greenberg 1990; Marra et al. 1993) and sexual habitat segregation on their wintering grounds (Ornat and Greenberg 1990; Sliwa 1991; Marra and Holberton 1998), also the result of behavioral dominance by older males (Marra 2000). Winter territoriality probably functions primarily to secure a dependable source of food over the winter period (Price 1981; Greenberg 1986), and secondarily to provide safe haven from predators and inclement weather. Regardless of cause, redstarts relegated to poor winter habitat (largely females) lose mass over winter, depart later on spring migration, and have lower annual survival (Marra et al. 1998; Marra and Holmes 2001). Thus, redstarts present a convenient case study with which to investigate broader issues of seasonal interactions; indeed, their dynamics motivated our thoughts on the subject.

In this chapter, we develop a population model that is motivated by the dynamics of American Redstarts but is applicable to many species with similar patterns of sexual habitat segregation on the wintering grounds (Marra and Holmes 2001). Through a series of simulations with this model, we investigate: (1) how the amounts of breeding and nonbreeding habitat interact to determine equilibrium population size; (2) the extent to which sexual habitat segregation in winter influences equilibrium population size and sex ratio; and (3) the importance of carry-over effects from the nonbreeding to the breeding season. The focus of this modeling work is not to make specific predictions about a particular population or species, but rather, to understand patterns of population dynamics driven by seasonal interactions.

METHODS

Model Description

We developed a matrix population model to describe a migratory bird species that experiences habitat limitation and segregation on both the breeding and nonbreeding grounds, with the potential for carry-over effects between seasons (28.2). Upon arrival at the wintering grounds, birds compete for territories in "good" habitat, which is limited and has a carrying capacity of K_{wg}; those that lose this competition must occupy territories in "poor" habitat, which is unlimited (if not actually unlimited, then practically so).

Fig. 28.2. Diagram of the stages in the annual cycle of a migratory songbird, as captured by the population model described in this chapter. The winter season encompasses two processes: competition for high-quality habitat upon arrival on the wintering grounds and winter mortality. The breeding season encompasses three processes: partitioning of breeding habitat by arrival time, reproduction, and summer mortality. The winter and breeding seasons are linked by migratory periods, which have mortality associated with them. See "Model Description" in the text for more details about this annual cycle.
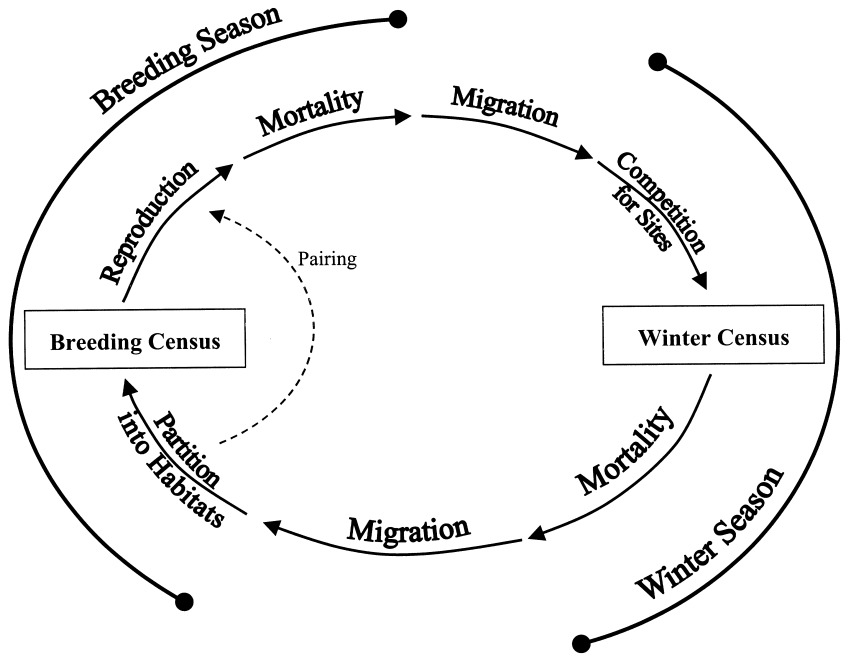
After all the birds have arrived and settled onto territories in year t, the population can be described as a vector

$$\mathbf{W}(t) = \begin{bmatrix} W_{mg}(t) \\ W_{mp}(t) \\ W_{fg}(t) \\ W_{fp}(t) \end{bmatrix} \qquad (1)$$

where W_{mg} is the number of males in "good" habitat, W_{fp} is the number of females in "poor" habitat, and so on. (In the description that follows, we drop the year-specific notation for simplicity of expression, thus referring to $\mathbf{W}(t)$ as $\mathbf{W}$, and similarly for other quantities. We bring back the year-specific notation at the very end.) These birds experience mortality over the winter season that is both sex- and habitat-specific. At the end of the winter season, the population structure is

$$\mathbf{W}' = \begin{bmatrix} s_{wmg} & 0 & 0 & 0 \\ 0 & s_{wmp} & 0 & 0 \\ 0 & 0 & s_{wfg} & 0 \\ 0 & 0 & 0 & s_{wfp} \end{bmatrix} \cdot \mathbf{W} \qquad (2)$$

where, for example, s_{wmg} is the winter survival rate for males in good habitat, and the prime-notation ($\mathbf{W}'$) is used to indicate the population structure post-winter. At the end of the winter season, birds migrate north to breeding grounds. Mortality during migration depends upon the sex of the bird and upon the winter habitat from which it leaves. Birds that spend the winter in poor habitat leave the wintering grounds later and in poorer condition (fig. 28.1). After spring migration, the structure of the population is

$$\mathbf{W}'' = \begin{bmatrix} s_{smg} & 0 & 0 & 0 \\ 0 & s_{smp} & 0 & 0 \\ 0 & 0 & s_{sfg} & 0 \\ 0 & 0 & 0 & s_{sfp} \end{bmatrix} \cdot \mathbf{W}' \qquad (3)$$

where s_{smg} is the survival rate over spring migration for males that came from good habitat, and the double-prime-notation ($\mathbf{W}''$) is used to indicate the population structure after spring migration.

The breeding ground contains two types of habitat, both of which are limited: the "source" habitat has a carrying capacity of K_{bc} (breeding ground, source habitat) pairs; the "sink" habitat, which is of lesser quality, has a carrying capacity of K_{bk} (sink) pairs. Because birds that wintered in good habitat arrive on the breeding grounds earlier, they fill the source habitat first. The number of females in source habitat is given by

$$B_{fc} = \begin{cases} W_{fg}'' + W_{fp}'' & \text{if } W_{fg}'' + W_{fp}'' < K_{bc} \\ K_{bc} & \text{otherwise} \end{cases} \qquad (4)$$

and the number of females in sink habitat is given by

$$B_{fk} = \begin{cases} 0 & \text{if } W_{fg}'' + W_{fp}'' < K_{bc} \\ W_{fg}'' + W_{fp}'' - K_{bc} & \text{if } K_{bc} \leq W_{fg}'' + W_{fp}'' < K_{bc} + K_{bk} \\ K_{bk} & \text{if } W_{fg}'' + W_{fp}'' \geq K_{bc} + K_{bk} \end{cases} \qquad (5)$$

Note that density dependence is implicit in equation (5): females displaced from sink habitat are presumed to die. This is a "ceiling" form of density dependence—no effect is evident until the number of arriving females exceeds the com-

bined carrying capacity of the source and sink habitats. The number of males in source habitat is described similarly,

$$B_{mc} = \begin{cases} W''_{mg} + W''_{mp} & \text{if } W''_{mg} + W''_{mp} < K_{bc} \\ K_{bc} & \text{otherwise} \end{cases} \quad (6)$$

but the number of males in sink habitat is limited by being able to find a mate, hence by B_{fk} rather than K_{bk}:

$$B_{mk} = \begin{cases} 0 & \text{if } W''_{mg} + W''_{mp} < K_{bc} \\ W''_{mg} + W''_{mp} - K_{bc} & \text{if } K_{bc} \le W''_{mg} + W''_{mp} < K_{bc} + B_{fk}. \\ B_{fk} & \text{if } W''_{mg} + W''_{mp} \ge K_{bc} + B_{fk} \end{cases} \quad (7)$$

In contrast to females, if the number of arriving males exceeds the carrying capacity or the number of females, the additional males do not die, but become "drain" males—non-territorial males that move around looking for a vacated territory or the potential for extra-pair copulation. Thus, the number of "drain" males is given by

$$B_{md} = \max(0, W''_{mg} + W''_{mp} - K_{bc} - B_{fk}). \quad (8)$$

Pairs formed from arriving males and females can be placed in eight classes, depending on whether the pair is in source or sink habitat, whether the male spent the previous winter in good or poor habitat, and whether the females spent the winter in good or poor habitat. Because birds coming from good winter habitat arrive on breeding grounds first, as many "good-good" pairs as possible form. Of all pairs in source habitat, the proportion composed of both a male and female from good habitat is

$$P_{cgg} = \begin{cases} 1 & \text{if } W''_{mg} > K_{bc} \text{ and } W''_{fg} > K_{bc} \\ \dfrac{\min(W''_{mg}, W''_{fg})}{\min(b_{mc}, B_{fc})} & \text{otherwise} \end{cases} ; \quad (9)$$

The proportion composed of a male from good winter habitat and a female from poor winter habitat is

$$P_{cgp} = \begin{cases} \dfrac{\min(W''_{mg}, B_{fc}) - W''_{fg}}{\min(B_{mc}, B_{fc})} & \text{if } W''_{mg} > W''_{fg} \text{ and } W''_{fg} < K_{bc}; \\ 0 & \text{otherwise} \end{cases} \quad (10)$$

The proportion composed of a "poor" male and a "good" female is

$$P_{cgp} = \begin{cases} \dfrac{\min(W''_{fg}, B_{mc}) - W''_{mg}}{\min(B_{mc}, B_{fc})} & \text{if } W''_{mg} > W''_{fg} \text{ and } W''_{mg} < K_{bc}; \\ 0 & \text{otherwise} \end{cases} \quad (11)$$

And the proportion composed of a male and female both from poor habitat can be found by subtraction,

$$P_{cpp} = 1 - P_{cgg} - P_{cgp} - P_{cpg}. \quad (12)$$

A similar logic is needed to determine the proportion of pairs, by class, in the sink habitat, but the number of cases is somewhat larger. Of all the pairs in sink habitat, the proportion composed of a male and female both from good winter habitat is

$$P_{kgg} = \begin{cases} 1 & \text{if } W''_{mg} \ge K_{bc} + K_{bk} \text{ and } W''_{fg} \ge K_{bc} + K_{bk} \\ 0 & \text{if } W''_{mg} \le K_{bc} \text{ or } W''_{fg} \le K_{bc} \\ \dfrac{\min(W''_{mg}, W''_{fg} - K_{bc})}{\min(B_{mk}, B_{fk})} & \text{otherwise} \end{cases} \quad (13)$$

The proportion composed of a "good" male and a "poor" female is

$$P_{kgp} = \begin{cases} 1 & \text{if } W''_{fg} < K_{bc} \text{ and } W''_{mg} \ge K_{bc} + K_{bk} \\ \dfrac{W''_{mg} - K_{bc}}{\min(B_{mk}, B_{fk})} & \text{if } W''_{fg} < K_{bc} \text{ and } K_{bc} < W''_{mg} < K_{bc} + K_{bk}; \\ \dfrac{\min(W''_{mg}, B_{fk} + K_{bc}) - W''_{fg}}{\min(B_{mk}, B_{fk})} & \text{if } K_{bc} < W''_{fg} < K_{bc} + K_{bk} \text{ and } W''_{mg} > W''_{fg} \\ 0 & \text{otherwise} \end{cases} \quad (14)$$

The proportion composed of a "poor" male and a "good" female is

$$P_{kgp} = \begin{cases} 1 & \text{if } W''_{mg} < K_{bc} \text{ and } W''_{fg} \ge K_{bc} + K_{bk} \\ \dfrac{W''_{fg} - K_{bc}}{\min(B_{mk}, B_{fk})} & \text{if } W''_{mg} < K_{bc} \text{ and } K_{bc} < W''_{fg} < K_{bc} + K_{bk}; \\ \dfrac{\min(W''_{fg}, B_{mk} + K_{bc}) - W''_{mg}}{\min(B_{mk}, B_{fk})} & \text{if } K_{bc} < W''_{mg} < K_{bc} + K_{bk} \text{ and } W''_{fg} > W''_{mg} \\ 0 & \text{otherwise} \end{cases} \quad (15)$$

And the proportion composed of a male and female both from poor habitat is

$$P_{kpp} = \begin{cases} 1 - P_{kgg} - P_{kgp} - P_{kpg} & \text{if } B_{mk} > 0 \text{ and } B_{fk} > 0. \\ 0 & \text{otherwise} \end{cases} \quad (16)$$

Thus, after the birds have settled into pairs, the population structure on the breeding ground (corresponding to the "breeding census" in fig. 28.2) is

$$\mathbf{B} = \begin{bmatrix} B_{mc} \\ B_{mk} \\ B_{md} \\ B_{fc} \\ B_{fk} \end{bmatrix}. \quad (17)$$

Fecundity rates for a pair depend on whether the pair is in source or sink habitat, and also on the composition of the pair with regard to habitat in the previous winter. This is the mechanism for a "carry-over effect"—individuals from good winter habitat arrive earlier and in better condition, and translate these advantages into increased production. The average fecundity for pairs in source and sink habitat is given by

$$
\begin{bmatrix} R_{\text{source}} \\ R_{\text{sink}} \end{bmatrix} = \begin{bmatrix} P_{cgg} & P_{cgp} & P_{cpg} & P_{cpp} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_{kgg} & P_{kgp} & P_{kpg} & P_{kpp} \end{bmatrix} \begin{bmatrix} R_{cgg} \\ R_{cgp} \\ R_{cpg} \\ R_{cpp} \\ R_{kgg} \\ R_{kgp} \\ R_{kpg} \\ R_{kpp} \end{bmatrix}
$$

(18)

where the R_i values are the habitat- and class-specific fecundities. The number of young produced is given by

$$
\mathbf{Y} = \begin{bmatrix} Y_{mc} \\ Y_{mk} \\ Y_{fc} \\ Y_{fk} \end{bmatrix} = \begin{bmatrix} 1-f & 0 \\ 0 & 1-f \\ f & 0 \\ 0 & f \end{bmatrix} \begin{bmatrix} \min(B_{mc}, B_{fc}) & 0 \\ 0 & \min(B_{mk}, B_{fk}) \end{bmatrix} \begin{bmatrix} R_{\text{source}} \\ R_{\text{sink}} \end{bmatrix}
$$

(19)

where f is the fraction of young that are female, and Y_{mc}, for instance, is the number of male young produced from source habitat.

Adult birds experience both sex- and habitat-specific mortality over the breeding season. At the end of the breeding season, the population structure is

$$
\mathbf{B}' = \begin{bmatrix} s_{bmc} & 0 & 0 & 0 & 0 \\ 0 & s_{bmk} & 0 & 0 & 0 \\ 0 & 0 & s_{bmd} & 0 & 0 \\ 0 & 0 & 0 & s_{bfc} & 0 \\ 0 & 0 & 0 & 0 & s_{bfk} \end{bmatrix} \cdot \mathbf{B}
$$

(20)

where, for example, s_{bmc} is the breeding season survival rate for males in source habitat. Following breeding, birds migrate south to the wintering grounds. Mortality during migration depends upon the sex of the bird and the breeding habitat it used. This structure can be used to portray any pattern in habitat-specific effects; for example, sink adults could have lower survival rates than source adults (perhaps because their food resources were poorer) or they could have higher survival rates than source adults (perhaps because they chose to expend less energy on producing young); in the simulations in this chapter, we assumed the former (see "Parameter Values" below) but the model is flexible in this regard. After fall migration, the structure of the adult population is

$$
\mathbf{B}'' = \begin{bmatrix} s_{fmc} & 0 & 0 & 0 & 0 \\ 0 & s_{fmk} & 0 & 0 & 0 \\ 0 & 0 & s_{fmd} & 0 & 0 \\ 0 & 0 & 0 & s_{ffc} & 0 \\ 0 & 0 & 0 & 0 & s_{ffk} \end{bmatrix} \cdot \mathbf{B}'
$$

(21)

where s_{fmc} is the survival rate over fall migration for males that came from source habitat. The young also experience mortality during fall migration that is sex- and habitat-specific, so that after fall migration, the young that arrive on the wintering grounds are described by

$$
\mathbf{Y}'' = \begin{bmatrix} s_{ymc} & 0 & 0 & 0 \\ 0 & s_{ymk} & 0 & 0 \\ 0 & 0 & s_{yfc} & 0 \\ 0 & 0 & 0 & s_{yfk} \end{bmatrix} \cdot \mathbf{Y}
$$

(22)

where s_{ymc} is the survival rate over fall migration for young males from source habitat (note that there is no vector $\mathbf{Y}'$ needed in this model). The population that arrives on the wintering grounds in composed of both adult and young

$$
\mathbf{A} = \begin{bmatrix} \mathbf{B}''_{5 \times 1} \\ \mathbf{Y}''_{4 \times 1} \end{bmatrix}.
$$

(23)

These birds compete for territories in "good" winter habitat, which is limited to K_{wg} individuals (note that this carrying capacity is measured in individuals, not pairs). Their ability to compete depends upon an intrinsic age-, sex-, and condition (habitat)-specific competitive factor (γ) and the number of birds in each class. Note that there is also a carry-over effect implicit in this competition if there is a difference in γ's based on breeding habitat. The number of birds in each class that successfully compete for good habitat is given by

$$
A_i^G = \frac{A_i \gamma_i}{\sum_i A_i \gamma_i} K_{wg}
$$

(24)

where i indexes the nine classes found in equation (23), with provisions made so that

$$
A_i^G \le A_i \text{ for all } i.
$$

(25)

The number of birds in each class that are relegated to poor habitat is found by subtraction,

$$
A_i^P = A_i - A_i^G.
$$

(26)

After the competition, the distinctions between young and adult, source and sink, are lost, so

$$
\begin{aligned}
W_{mg} &= A_{mc}^G + A_{mk}^G + A_{md}^G + A_{ymc}^G + A_{ymk}^G \\
W_{mp} &= A_{mc}^P + A_{mk}^P + A_{md}^P + A_{ymc}^P + A_{ymk}^P \\
W_{fg} &= A_{fc}^G + A_{fk}^G + A_{yfc}^G + A_{yfk}^G \\
W_{fp} &= A_{fc}^P + A_{fk}^P + A_{yfc}^P + A_{yfk}^P
\end{aligned}
$$

(27)

and finally,

$$\mathbf{W}(t+1) = \begin{bmatrix} W_{mg}(t+1) \\ W_{mp}(t+1) \\ W_{fg}(t+1) \\ W_{fp}(t+1) \end{bmatrix} = \begin{bmatrix} W_{mg} \\ W_{mp} \\ W_{fg} \\ W_{fp} \end{bmatrix} \qquad (28)$$

where we now bring back the year-specific notation to indicate that a year has passed.

Parameter Values

As described above, this model requires 43 parameters: 22 survival rates, eight fecundity rates, nine competition parameters, the fraction of young that are female, and three carrying capacities. If our purpose were prediction or assessment for a particular species, careful attention to formal parameter estimation would be critical; but for the purposes of understanding the patterns in the dynamics of the model, point estimates for parameters are less important than the patterns among them. Thus, while the American Redstart provided a guidepost for the articulation of model parameters, the following section should not be viewed as a formal exercise in estimation.

We assumed that winter survival rates did not differ by sex or habitat (Marra and Holmes 2001), but that spring migration survival rates were lower for birds from poor habitat than good habitat (table 28.1). During the breeding season, we assumed that survival did not differ by sex, but did de-

pend on habitat, with birds in sink habitat having lower survival rates than birds in source habitat, and drain males having the lowest survival rates (table 28.2). A similar pattern was used for fall migration survival rates, except we assumed that drain males were more similar to source males because drain males do not incur any costs of reproduction (table 28.2). We assumed that the survival rates of young during fall migration were the same as adults from the same habitat (table 28.2). Note that young are not kept separate in the model once they arrive and settle on wintering habitat.

We simplified the eight fecundity rates into three parameters: a base rate, a habitat effect, and a carry-over effect (table 28.3). Note that these fecundity rates are the number of young per pair that are alive at the end of the breeding season; thus, they incorporate all components of productivity, including fledgling survival. We set the base rate at 1.8 young per pair in source habitat, and assumed that fecundity was half that in sink habitat (Sherry and Holmes 1997). To simplify the carry-over effect of winter habitat on subsequent productivity, we assumed that for each member of a pair that spent the previous winter in poor habitat, the fecundity of the pair was reduced by a factor c (table 28.3). Thus, with a carry-over effect $c = 2$, a pair composed of a male from good habitat and a female from poor habitat would have a fecundity half that of a "good-good" pair, and a "poor-poor" pair would have a fecundity half that again. We assumed that the sex ratio of young was 1:1 (thus, $f = 0.5$).

We simplified the nine competitive factors into three effects: the competitive ability for good winter habitat of birds that bred in or fledged from source habitat relative to those from sink habitat; the relative competitive ability of young compared with adults; and the relative competitive ability of males compared with females (table 28.4). Birds from sink habitat were assumed to have one-tenth the competitive ability of birds from source habitat, owing possibly to a later arrival date. Likewise, young were assumed to have one-fifth the competitive ability of adults. To explore the effect of male-biased competition for good winter habitat, we defined a male dominance parameter, γ, that we allowed to vary from 1 (equal competitive ability between males and females) to 5 (males five times more competitive than females). Marra and Holmes (2001) found a male-to-female ratio of 6:4 in good winter habitat for American Redstarts. This is not

Table 28.1 Winter survival rates and spring migration survival rates used in the model, by sex and habitat type

		Winter Survival		Spring Migration Survival
Males on good habitat	s_{wmg}	0.80	s_{smg}	0.90
Males on poor habitat	s_{wmp}	0.80	s_{smp}	0.80
Females on good habitat	s_{wfg}	0.80	s_{sfg}	0.90
Females on poor habitat	s_{wfp}	0.80	s_{sfp}	0.80

Table 28.2 Breeding season survival rates and fall migration survival rates used in the model, by sex, age, and habitat type

		Breeding Season Survival		Fall Migration (adults)		Fall Migration (young)
Males on source habitat	s_{bmc}	0.95	s_{fmc}	0.80	s_{ymc}	0.80
Males on sink habitat	s_{bmk}	0.85	s_{fmk}	0.75	s_{ymk}	0.75
Drain males	s_{bmd}	0.80	s_{fmd}	0.80	—	—
Females on good habitat	s_{bfc}	0.95	s_{ffc}	0.80	s_{yfc}	0.80
Females on poor habitat	s_{bfk}	0.85	s_{ffk}	0.75	s_{yfk}	0.75

Table 28.3   Fecundity rates by habitat and pair-class

Habitat	Pair-class	Parameter	Formula	$c = 1$	$c = 2$
Source	Good-Good	R_{cgg}	1.8	1.8	1.8
	Good-Poor	R_{cgp}	$1.8/c$	1.8	0.9
	Poor-Good	R_{cpg}	$1.8/c$	1.8	0.9
	Poor-Poor	R_{cpp}	$1.8/c^2$	1.8	0.45
Sink	Good-Good	R_{kgg}	0.9	0.9	0.9
	Good-Poor	R_{kgp}	$0.9/c$	0.9	0.45
	Poor-Good	R_{kpg}	$0.9/c$	0.9	0.45
	Poor-Poor	R_{kpp}	$0.9/c^2$	0.9	0.225

Note: In the simulations described in this chapter, for each member of a pair that spends the winter on poor habitat, the fecundity is reduced by a factor c. This factor represents the strength of the carry-over effect. The fecundities are shown for two values of the carry-over effect: no effect ($c = 1$) and a strong effect ($c = 2$).

a direct measure of competitive ability because the sex ratio depends on the overall sex ratio in the population and the differential survival rates between the sexes, as well as the relative competitive abilities, but it is nevertheless a rough indication of the level of competition. We chose a range approximately twice as large as this observation to capture a potential range for the male dominance parameter. Note that we did not investigate a range of values for the other two competitive effects (source vs. sink individuals, young vs. adults), but such an investigation is warranted.

In the simulations with the model, a wide range of values was explored for two of the three carrying capacities (K_{bc} and K_{wg}). The third carrying capacity (K_{bk}, the capacity of sink breeding habitat) was set at a level (10,000) much higher than the other carrying capacities, so that it was effectively unlimited.

Simulations

We performed three sets of simulations, all designed to look at properties of the model at equilibrium. To calculate equilibrium results, we iterated the model through time with a fixed set of parameters, until population vectors during the

breeding and winter seasons stabilized. Typically, equilibrium was reached within 50 simulated annual cycles, but we always ran the model for 300 annual cycles to be certain.

The three sets of simulations were designed to examine, in turn, the effects of three dynamics: the relative amounts of breeding and winter carrying capacity; sexual habitat segregation; and winter-to-summer carry-over effects. In the first simulation, we varied carrying capacities of source breeding and good winter habitat and examined the resulting equilibrium population size on the breeding ground. For this simulation, we held the carry-over effect at $c = 1$, and the male dominance parameter at $\gamma = 5$. From the results of this simulation, we chose three combinations of carrying capacities, all of which produced an equilibrium breeding-ground population size of 500 birds: a summer-limited case ($K_{bc} = 205$ pairs, $K_{wg} = 900$ individuals); an intermediate case ($K_{bc} = 224$ pairs, $K_{wg} = 580$ individuals); and a winter-limited case ($K_{bc} = 800$ pairs, $K_{wg} = 485$ individuals). We used these three cases in the second and third simulations. In the second simulation, we varied the male dominance parameter, held the carry-over effect constant ($c = 1$), and looked at the resulting equilibrium sex ratio (male:female) during the breeding season. In the third simulation, we varied the

Table 28.4   Competitive factors by habitat, sex, and age

Sex and Age	Habitat	Parameter	Formula	$\gamma = 1$	$\gamma = 5$
Adult male	Source	γ_1	1	1	1
	Sink	γ_2	0.1	0.1	0.1
	Drain	γ_3	0.01	0.01	0.01
Adult female	Source	γ_4	$1/\gamma$	1	0.2
	Sink	γ_5	$0.1/\gamma$	0.1	0.02
Young male	Source	γ_6	0.2	0.2	0.2
	Sink	γ_7	0.01	0.01	0.01
Young female	Source	γ_8	$0.2/\gamma$	0.2	0.04
	Sink	γ_9	0.01	0.01	0.01

Note: For the simulations in this chapter, these competitive factors are assumed to be governed by a male dominance parameter γ—the stronger this factor, the greater the competitive edge males have over females for good winter habitat. With $\gamma = 1$, there is no difference between the sexes in competition for good winter habitat; with $\gamma = 5$, the odds of a single male outcompeting a single female are 5:1.

strength of the carry-over effect, held the male dominance parameter constant ($\gamma = 5$), and looked at the resulting equilibrium breeding population size.

RESULTS

Equilibrium population size on breeding grounds ($\Sigma B = B_{mc} + B_{mk} + B_{md} + B_{fc} + B_{fk}$) varied as a function of the carrying capacities of source breeding habitat (K_{bc}, measured in pairs) and good wintering habitat (K_{wg}, measured in individuals) (fig. 28.3). This variation indicates different conditions for winter and breeding limitation (fig. 28.3). The equilibrium surface shows two pronounced areas: one (marked "W") where the population is winter limited, and one (marked "B") where the population is breeding limited, with a transition zone ("T") between them. In the area marked "W," equilibrium population size increases (or decreases) as the amount of good winter habitat (hence the carrying capacity K_{wg}) increases (or decreases), regardless of changes in the amount of source breeding habitat (hence carrying capacity K_{bc}). In this area, equilibrium population size does not change with a change in the amount of source habitat, provided the amount of good winter habitat is held constant. Thus, the population must be winter limited, because only changes in winter habitat can change the equilibrium population size. A similar argument shows why the population is breeding limited at the point marked "B." In either case, sufficient increase in suitable habitat in the limiting season eventually causes the limitation to switch to the other season. For instance, as the amount of source breeding habitat increases from point "B," while holding winter habitat constant, equilibrium population size increases, *up to a point.* Beyond that, the population becomes winter limited, and further increases in breeding habitat will not change the equilibrium

population size. The results for equilibrium *winter* population size (not shown) are qualitatively similar to those for breeding population size (fig. 28.3).

The dynamics in the transition zone ("T" in fig. 28.3) between the winter- and breeding-limited regions are due to subtle interactions between the seasons. In this region, the population is largely breeding limited but is affected slightly by the amount of winter habitat. The seasonal interaction can be understood by considering the bold line in fig. 28.3, along which source breeding habitat increases while good winter habitat is held constant (at $K_{wg} = 900$ individuals). This slice through the three-dimensional surface in fig. 28.3 is shown in two dimensions in fig. 28.4, as the top line in the upper panel. The remaining lines in the upper panel divide the total population into source, sink, and drain individuals, and the lower panel shows the corresponding equilibrium *winter* population size, divided into individuals in good and poor habitats. Initially, as the capacity of source breeding habitat (hence carrying capacity K_{bc}) increases, the equilibrium summer (upper panel) and winter (lower panel) population sizes increase as well, because under these circumstances, the population is breeding-season limited. Left of reference line a, where the population is breeding limited, all individuals are able to occupy good winter habitat (see lower panel), and enough birds return to the breeding grounds that some must spill over into sink habitat (see upper panel). At a certain point (reference line a), there is enough source habitat that the good winter habitat fills (its carrying capacity is 900). With continued increases in source habitat, birds must compete for good winter habitat and some must spill over into poor winter habitat (lower panel, between lines a and b). Two things begin to happen on the breeding grounds (upper panel): first, because survival during spring migration is lower for birds from poor winter habitat, proportionally fewer birds return to the breeding
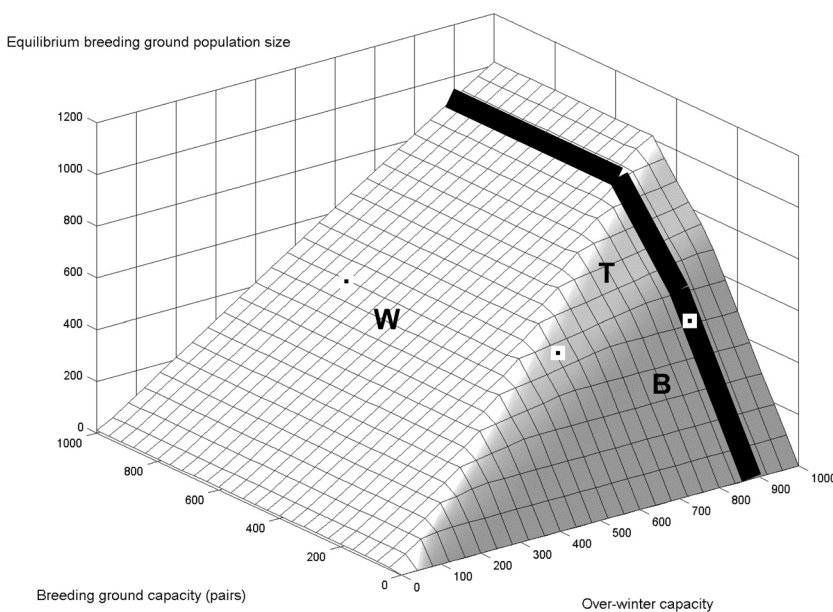

Equilibrium breeding ground population size

Breeding ground capacity (pairs)

Over-winter capacity

Fig. 28.3. Equilibrium population size on the breeding grounds (ΣB, equation 28.17[**AQ1**]) as a function of the carrying capacities of source breeding habitat (K_{bc}, in pairs) and good winter habitat (K_{wg}, in individuals). "W" refers to the conditions under which the population is winter limited, "B" to conditions of breeding-season limitation, and "T" to a transition zone between the two. The bold line shows a slice through this curve when K_{wg} is held constant at 900; this is shown in more detail in fig. 28.4. The three squares represent pairs of carrying capacities for which the equilibrium breeding population size is 500, but which differ in being winter limited, summer limited, or intermediate; these are the three cases shown in figs. 28.5 and 28.6. The equilibrium population sizes in this figure were generated with $c = 1$ and $\gamma = 5$.

Fig. 28.4. Equilibrium breeding (ΣB, equation 17) and winter (ΣW, equation 1) population sizes as a function of the carrying capacity of source breeding habitat (K_{bc}), with the carrying capacity of good winter habitat (K_{wg}) held constant at 900. The regions between the curves in the first graph show the equilibrium population sizes in source, sink, and "drain" breeding habitats, males and females combined. The regions between the curves in the second graph show the equilibrium population sizes in good and poor winter habitats, males and females combined. The references lines (a, b, and c) mark important transition points in the dynamics, generated by seasonal interactions (see "Results").
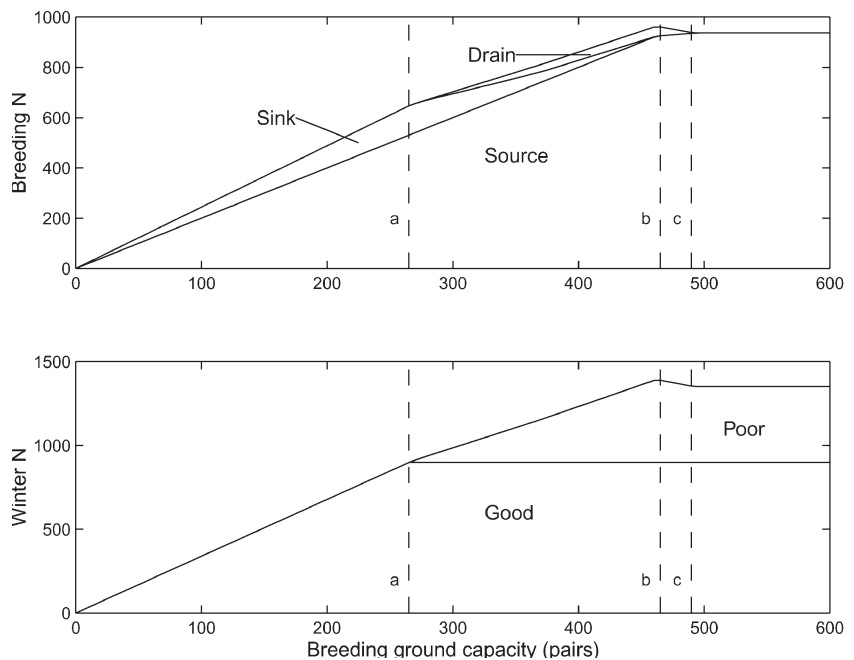
grounds and the use of sink habitat decreases; second, because males compete more effectively for the good winter habitat, the sex ratio shifts, and the number of "drain" (unpaired) males increases. At reference line b, the average survival rate of females has decreased enough that all the females that return to the breeding grounds can find territories in source habitat; thus there are no pairs in sink habitat (upper panel). Up to this point, the sex ratio in the source breeding habitat is 1:1—all males in source habitat find a mate; but the overall sex ratio is male biased, due to the "drain" males. But beyond line b, as the average survival rate of females continues to drop (because a greater proportion of them are in poor winter habitat), there are not enough females to mate with the males, even in source habitat. With continued increases in source habitat, all the males can find a territory in source habitat, even though not all find mates. At reference line c, the average winter survival rates have decreased to the point that continued increases in source breeding habitat produce no further increases in equilibrium population size (both upper and lower panels). Beyond this, the population is entirely winter limited. The conditions between reference lines a and c in fig. 28.4 correspond to the transition zone in fig. 28.3. Equilibrium sex ratio on the breeding grounds is influenced by the male dominance parameter on the winter grounds (fig. 28.5). If a population is winter limited, and the male dominance parameter is greater than 1, a greater proportion of females will be forced into the poor winter habitat. This lowers the average spring migration survival rates of females relative to males, resulting in a male-biased sex ratio on the breeding grounds and, in turn, a male-biased sex ratio on the wintering grounds the following year. As the strength of the male dominance parameter increases, so does the bias in the sex ratio. On the other hand, if a population is summer lim-

ited, then competition for good winter habitat becomes unimportant, and the male dominance parameter has no effect on the sex ratio. Note that the 1:1 sex ratio seen in fig. 28.5 is a consequence of the base survival rates being equal between the sexes; this need not be the case. If sex-specific survival rates are caused by factors other than competition for good winter habitat, the base sex ratio would still depart from 1:1; however, the sex ratio would not be affected by the dominance parameter in a summer-limited population. Populations in the transition zone ("T") show an intermediate effect of the male dominance parameter on sex ratio.

Equilibrium breeding population size ΣB can be influenced by the strength of the carry-over effect (c), particularly when the population is winter limited (fig. 28.6). The carry-over effect is the ratio of productivity of individuals from good versus poor winter habitat. For instance, with a carry-over effect of 2, a "good-good" pair has twice the productivity of a "good-poor" or "poor-good" pair, and four times the productivity of a "poor-poor" pair. In a winter-limited population, as the strength of this carry-over effect increases, the equilibrium population size decreases, because the net productivity of the population decreases. In a summer-limited population, no such effect is observed, because there are no birds spending the winter in poor habitat (see fig. 28.4, lower panel, left of line a). For populations in the transition zone ("T" in fig. 28.3, and between lines a and c in fig. 28.4), the effect is intermediate, because a smaller portion of the population spends the winter in poor habitat.

DISCUSSION

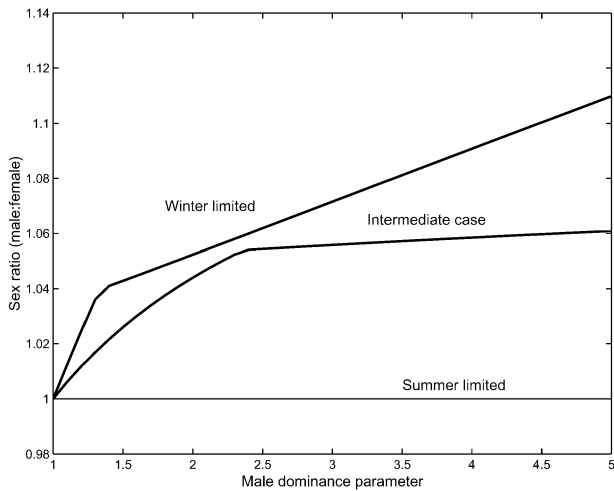Modeling provides an indispensable tool for identifying critical aspects of an organism's annual cycle and understand-

Fig. 28.5. Equilibrium sex ratio (male:female) on the breeding grounds as a function of the male dominance parameter on the wintering grounds (γ). The carry-over effect (c) is held at 1. The three cases correspond to the squares in fig. 28.3: a winter-limited case ($K_{bc} = 800$ pairs, $K_{wg} = 485$ individuals); an intermediate case ($K_{bc} = 224$ pairs, $K_{wg} = 580$ individuals); and a summer-limited case ($K_{bc} = 205$ pairs, $K_{wg} = 900$ individuals).

ing the interactions among them. To date, few attempts have been made to develop either theoretical or empirical population models for migratory birds that explicitly incorporate seasonal dynamics; as a result, we have a limited set of tools available for understanding the factors that drive the dynamics of such populations (but see Goss-Custard et al. 1995a, 1995b, 1995c, 1995d). Undertaking such model development is daunting, however, because of the practical difficulties associated with parameter estimation. Migratory birds move over large geographic areas, often thousands of miles between breeding, stopover, and winter sites. Such behavior makes acquiring demographic information
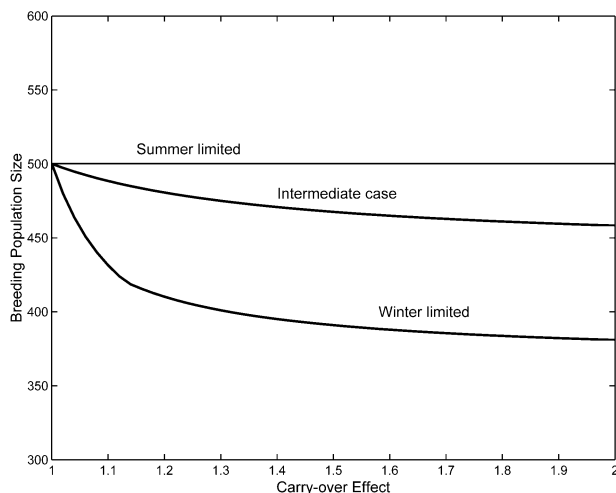

Fig. 28.6. Equilibrium breeding population size (ΣB, equation 17) as a function of the strength of the carry-over effect (c), with the male dominance parameter held at $\gamma = 5$. The three cases are as described in the legend of fig. 28.5 (and depicted in fig. 28.3).

from the entire annual cycle extremely difficult (but see Sillett and Holmes 2002). Despite these issues, developing theoretical models remains a valuable exercise for generating research hypotheses, setting conservation priorities, assessing management options, and identifying which parameters have the greatest potential impact on population dynamics.

In this chapter, we developed a theoretical population model to help understand the significance of density dependence, behavioral dominance, and carry-over effects in the annual cycle of a long-distance migratory bird. Although much of our model development and results were based on information collected from American Redstarts, there are several similarities between this and other species of migratory birds allowing for broader generalization. One of the primary mechanisms driving the dynamics of this model is the dominance behavior in winter and summer. To date, 16 species of migratory songbirds have been shown to exhibit sexual habitat segregation on their nonbreeding grounds (e.g., Nisbet and Medway 1972; Ornat and Greenberg 1990; Greenberg et al. 1997; P. P. Marra, unpubl. data), a spacing pattern probably caused by dominance (Marra 2000). Furthermore, most species of songbirds also exhibit some form of dominance-mediated spacing pattern during the breeding season. Because dominance-mediated spacing systems and their associated consequences for physical condition and survival appear to be relatively common, the model we present here may well be applicable to other migratory bird species.

Seasonal Population Limitation

To address the issue of seasonal population limitation, we varied the capacities of source breeding and good winter habitat, and looked at the resulting equilibrium population sizes throughout the annual cycle. We found large sets of conditions under which the population was entirely limited by either winter or breeding habitat (fig. 28.3). A similar question was investigated by Dolman and Sutherland (1994) and applied specifically to Oystercatchers (*Haematopus ostralegus*) (see also Sutherland and Dolman 1994; Goss-Custard et al. 1995a, 1995b, 1995c, 1995d; Sutherland 1996, 1998). Our results (fig. 28.3) differ from those of Dolman and Sutherland (1994:S41, their fig. 2a): region "M" of their figure corresponds to region "B" or ours; and their region "P" corresponds to our region "W"; but between those regions, the results of Dolman and Sutherland (1994) show a much more gradual transition, such that equilibrium population size changes with change in the amount of either winter or breeding habitat. These differences are due to the nature of the density dependence implicit within each model. In the Oystercatcher model, productivity and survival decreased gradually with increases in density. This form of density dependence might imply a crowding mechanism, such that average mortality and productivity decrease with each additional individual (Fretwell 1972). In our model, we used a site-dependent form of density dependence (Rodenhouse et al. 1997). Under this mechanism, once the source breeding

or good winter habitat is filled, each additional bird that attempts to settle will be forced into the next best available habitat, resulting in a sharp change in the consequences for those birds forced into suboptimal habitat. We have no crowding mechanism per se implicit in our model. A more detailed site-dependent model could allow for a continuous range of habitat quality; such a model might produce results more like those of Dolman and Sutherland (1994), since there would be a gradual change in the consequences for each additional bird in the population. In reality, multiple mechanisms probably interact to regulate population size in migratory birds (Rodenhouse et al. 2003), a dynamic that might further change the nature of density dependence. The critical point here is that the dominant mechanism for density dependence can strongly affect the nature of seasonal limitation. The importance of the functional form of density dependence, as an expression of the mechanism, has been demonstrated for other applications of population biology (Runge and Johnson 2002).

The potential importance and subtlety of population-level seasonal interactions are illustrated in fig. 28.4. Especially in the "transition" zone, an understanding of dynamics in any one season requires knowledge about how it interacts with processes in other seasons. For instance, as in Sutherland (1996), loss of winter habitat does not result in as severe a decline in equilibrium population size as might otherwise be expected, because increased production (due to density dependence on the breeding grounds) partially offsets the impact of the habitat loss. Understanding seasonal compensation thus requires understanding how the seasons interact with one another through population-level effects, especially as mediated by seasonal density-dependent processes.

Direct study of the form and strength of density dependence during a particular season would require formal estimates of seasonal survival (through, say, mark-recapture or radio-telemetry methods) in conjunction with estimates of density, over a long-enough period to observe a range of densities. Several such studies of seasonal survival have been conducted for waterfowl (e.g., Blohm et al. 1987; Reinecke et al. 1987), but density has not been measured, and the survival rates have typically varied so little that a relationship with density would have been undetectable. Sillett and Holmes (2002) estimated seasonal survival rates for Black-throated Blue Warblers, but found little evidence for density-dependent survival (Sillett and Holmes, Chap. 32, this volume). Goss-Custard et al. (1995d) have used some clever indirect methods to develop an estimate for nonbreeding-season density dependence, based on game theory models combined with data from measures of individual variation in competitive abilities (Dolman and Sutherland 1994; Goss-Custard et al. 1995a, 1995b; Sutherland 1996, 1998). This estimate, however, was generated from one research site and little is known about how this relationship varies geographically. Our modeling work, as well as that of Dolman and Sutherland (1994), suggests that understanding density dependence during the nonbreeding season could

be critical to understanding the population dynamics of long-distance migratory birds. This, in turn, suggests that new research is needed that quantifies the density dependence of nonbreeding-season survival (during the stationary and migratory periods) for a variety of avian taxa over large geographic spatial scales.

Sex Ratio Dynamics

The sex ratio dynamics throughout the annual cycle also need to be understood in the context of the interactions between seasons. Our results show that the equilibrium sex ratio on the breeding grounds can be influenced by male dominance on winter grounds. The sex ratio, however, is sensitive to the relative competition parameters only in a winter-limited population, because only then will there be consequences to female survival. These results may be particularly important for understanding the dynamics of redstarts and other species that show sexual habitat segregation. American Redstarts exhibit age-specific habitat segregation on their breeding grounds, and sex and age-specific habitat segregation on their wintering grounds, all known to be induced by the dominance behavior of males (Marra 2000). Such year-round intraspecific competition may be the primary behavioral mechanism driving the distribution of redstarts across the landscape. Ultimately, the consequences of this distribution depend on the relative amounts of suitable breeding and wintering habitats. Because male redstarts are behaviorally dominant over females during winter and exclude them into poor habitat, where their fitness may be lower, dominance behavior may play an integral role in determining the population sex ratio. Thus, when winter is the limiting season, limitation may act primarily through females, influencing population dynamics by reducing the number of females available for breeding (Marra and Holmes 1997, 2001).

It is important to note that simply observing a biased sex ratio on the breeding grounds is not evidence for intraspecific competition in the winter. Male-biased sex ratios could also be due to higher female mortality during the breeding season (Trivers 1972; Breitwisch 1989) or at any other point during the annual cycle. Intraspecific competition on the wintering grounds would be suggested by a shift in sex ratio following a change in the availability of good winter habitat. For example, if the sex ratio became male biased as good winter habitat was lost, that would suggest not only that the population was winter limited, but also that there was competition between the sexes on the winter grounds. Finally, note that the ratio of males to females in good winter habitat or in poor winter habitat is not simply a function of the relative competition parameters; it is a complex function of the primary sex ratio, the survival rates in good versus poor winter habitat, the relative survival rates of males and females in the rest of the annual cycle, and the relative amounts of habitat available on the breeding and wintering grounds.

Carry-Over Effects

Seasonal population dynamics can also interact through carry-over mechanisms that involve the fitness of individual birds. Our results show that carry-over effects can be substantial, but only if the population is limited in the season when the carry-over originates. Note that this carry-over effect can interact with the seasonal compensation effect: in the "transition" zone (fig. 28.6, intermediate case), the impact of the carry-over effect is moderated by the density dependence on the breeding grounds. A stronger carry-over effect leads to lower production, hence, lower equilibrium population size; but a lower population size also leads to increased production. Thus, the carry-over effect is partially offset. Again, to understand the carry-over dynamics or to be able to predict their effects, it is critical to understand them in the context of the annual cycle and all the other seasonal interactions. This implies that assigning causation for particular phenomena may require understanding events in the prior period, and for migratory birds, this could mean thousands of kilometers away from the point of measurement. Although this discussion implies that carry-over effects can interact with density dependence to affect population regulation, it does not follow that carry-over effects are a necessary condition for regulation. For instance, in the Black-throated Blue Warbler, which does not exhibit dramatic sexual habitat segregation and does not seem to be strongly limited by events on winter quarters, Sillett and Homes (Chap. 32, this volume) show that a population can be regulated solely by density dependence operating within the breeding season. Our point is just that carry-over effects *can* influence regulation, and we have only begun to scratch the surface of how to measure and understand the significance of carry-over effects for migratory birds (Marra et al.1998; Norris et al. 2004; Webster and Marra, Chap. 16, this volume; Szép and Møller, Chap. 29, this volume). We believe it is important to frame future research efforts on carry-over effects in the context of seasonal interactions.

We have focused our attention on a winter-to-summer carry-over effect, but the model also contains a summer-to-winter carry-over effect, the dynamics of which we have not yet explored. Because the model allows sink individuals to differ from source individuals in being able to compete for good winter habitat (through differential competitive factors, i.e., the γ_i's in equation 24), the habitat conditions of birds on the breeding grounds carry over to affect survival during winter. The strength of this summer-to-winter carry-over effect could be expressed as the ratio of competitive factors for source individuals to those for sink individuals. In the simulations shown herein, that ratio was fixed at 10:1; an interesting extension would be to explore the sensitivity of the equilibrium population sizes to this ratio.

FUTURE DIRECTIONS

We have shown that: (1) the relative amounts of breeding and wintering habitat strongly affect both equilibrium population size and sex ratio; (2) sex ratio dynamics, as mediated by behavioral dominance, can affect all other aspects of population dynamics; and (3) carry-over effects can play a critical role in driving population dynamics. The implications of these results are profound. To understand how populations are regulated we must consider carry-over effects as well as density-dependent mechanisms acting year-round. Otherwise, conclusions about the mechanisms driving population dynamics and predictions about future changes may be misleading. Moreover, for conservation of migratory species to be effective in the event of a population decline, intervention measures will depend on understanding where and how the population is limited.

But, we have much work to do if we hope to understand the nature of population limitation for migratory birds. First, we need to undertake the challenging work of obtaining direct estimates for several population parameters. We need more estimates for habitat-specific survival during the nonbreeding period, and these estimates should be measured throughout the winter ranges of particular species. We need estimates of the strength and functional form of density dependence during the breeding and wintering periods, either through long-term observational studies that quantify productivity and survival in relation to density; or through experimental studies that manipulate density and measure the impacts on productivity and survival. Second, we need a better understanding of how events during migration and stopover affect individual and population-level processes, and how migration events connect breeding and nonbreeding periods (DeSante 1995; Sherry and Holmes 1995; Sillett and Holmes 2002). It is generally accepted that density-independent factors are more significant than density-dependent processes for migratory birds during migration, but little is known definitively about this period (Sillett and Holmes 2002, Chap. 32, this volume). Direct estimation of survival during migration would be valuable, especially if it could be tied to habitat in the preceding stationary period to elucidate any carry-over effects. Better estimates of population connectivity among the periods of the annual cycle will ultimately bring us far in our pursuit of understanding carry-over effects and population dynamics. The challenge, of course, with the migration and connectivity questions, is how to follow individuals across vast geographic distances.

Regarding the model we have presented in this chapter, our analysis of its properties has been admittedly cursory. Greater understanding of the population dynamics implied by this model may help to motivate and focus additional field research. Several details invite further exploration: (1) In the transition zone ("T" in fig. 28.3), where seasonal compensation is acting, how is the carry-over effect moderated? (2) Likewise, how does seasonal compensation interact with the sex ratio dynamics induced by behavioral dominance? (3) What hypotheses about the effects of habitat loss, management, or enhancement can be generated by this model and tested in the field? (4) Which general results

in this chapter are not sensitive to the particular mechanisms of density dependence or carry-over?

In addition to further theoretical exploration of the model presented in this chapter, there is much value in developing an empirical application of it for a particular species. Such development may elucidate the challenges of parameter estimation, motivate development of new field studies for estimation, and allow us to understand the conservation needs of that species in greater detail.

ACKNOWLEDGMENTS

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