OIKOS 109: 178–186, 2005

Carry-over effects and habitat quality in migratory populations

D. Ryan Norris

Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. – Oikos 109: 178–186.

Determining the factors that influence migratory population abundance has been constrained by the inability to connect events in different periods of the annual cycle. Carry-over effects are events that occur in one season but influence individual success the following season and recent empirical evidence suggests that they may play an important role in migratory population dynamics. Using a long distance migratory shorebird as an example, I incorporate carry-over effects and changes in the relative amount of habitat quality into a density-dependent equilibrium population model. The model uses the example where the quality of habitat on the wintering grounds (nonbreeding season) influences breeding output the following summer (breeding season). Carry-over effects, however, may be manifested in a number of other ways that could influence population dynamics. In the simulations, population declines occur when habitat is lost on the wintering grounds. However, results show that carry-over effects can magnify these declines when a disproportionate amount of high quality habitat is lost the previous winter. Simulations also show that carry-over effects can have a relative, positive impact on population size when the majority of habitat that is lost in the previous season is low quality. In this case, the carry-over interacts with density-dependence the following season producing an additive and positive effect, buffering the population from severe declines. To predict changes in population size of migratory animals, it will be important to determine (i) which demographic factors in which season produce strong carry-over effects and, (ii) not just the amount, but the relative quality of habitat that is lost. If carry-over effects are significant, they could potentially mitigate 'seasonal compensation effects' from density-dependence, leading to exacerbated population declines.

D. R. Norris, Dept of Biology, Queen's Univ., Kingston, Ontario, Canada K7L 3N6 (ryann@biology.queensu.ca). Present address: Centre for Applied Conservation Research, Forest Sciences Centre, Univ. of British Columbia, 3041-2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4.

Population abundance in migratory animals is controlled by a combination of factors during different periods of the annual cycle (Sherry and Holmes 1996, Newton 2004). Predicting the factors that influence population dynamics, however, has been difficult because many species have breeding and nonbreeding ranges that are separated by large geographic distances. For migratory birds, determining the relative importance of factors at different stages of the annual cycle has been the focus of decades of research (Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995, Greenberg and Marra 2005), culminating in the development of models designed to predict population changes (Dolman and Sutherland 1994, Durell et al. 1997, Baillie et al. 2000, Pettifor et al. 2000, Zanette 2000).

The relationship between population abundance and the annual cycle in migratory animals, however, is probably more complex than previously thought (Sillett et al. 2000, Webster et al. 2002). Recent evidence suggests that carry-over effects, events in one season that produce residual effects on individuals the following season, can have a large impact on migratory

Accepted 10 September 2004

ISSN 0030-1299

populations. For example, American redstarts (*Setophaga ruticilla*) originating from high quality tropical winter habitat arrive earlier and have higher reproductive success on the temperate breeding grounds than individuals coming from low quality winter habitat (Marra et al. 1998, Norris et al. 2004). Gill et al. (2001) also found that black-tailed godwits (*Limosa limosa*) arriving early on the Icelandic breeding grounds were more likely to originate from higher quality habitat the previous winter.

Carry-over effects that occur at the individual level may have significant consequences at the population level. For example, loss of high quality habitat on the wintering grounds would not only increase mortality but could also result in a greater proportion of individuals over-wintering in poor quality habitat. As a result of a carry-over effect, the population would experience a decrease in per capita reproductive output the following season, resulting in a further reduction in population size. A decrease in the number of individuals on the breeding grounds (as a result in winter habitat loss), however, can also have the opposite effect on population size: fewer individuals result in an increase in per capita reproductive success through density-dependence. To distinguish this phenomenon from the population-level consequences of a carry-over effect, I term this process the 'seasonal compensation effect' ('Model development' for further discussion).

In contrast, via a carry-over effect, loss of primarily low quality habitat on the wintering grounds could have a positive impact on population size relative to losing high quality habitat. In this case, a greater proportion of individuals are originating from high quality winter habitat, increasing per capita reproductive success the following summer. In this case, the seasonal compensation effect (density-dependence on the breeding grounds) acts in concert with the carry-over effect, buffering populations from habitat loss the previous season.

In this paper, I examine these scenarios by incorporating carry-over effects and habitat quality into a density-dependent equilibrium population model (Fretwell 1972, Sutherland 1996). Using a long distance migratory shorebird, the oystercatcher (*Haematopus ostralegu*), as an example, I examine the contribution of carry-over effects to population change at different degrees of absolute habitat loss and at different proportions of habitat quality. I demonstrate how a carry-over effect can exacerbate or buffer population declines depending on the proportion of high quality habitat that is lost the previous season.

Model development

The following model is designed to represent a simplified migratory animal population with two seasons during the annual cycle: winter (nonbreeding) and summer (breeding) and two habitat types (high and low quality) on the wintering grounds in which individuals follow an ideal-despotic distribution (e.g. territorial). It is assumed that each of these habitat types initially occur in equal proportions. A schematic diagram of the entire model is presented in Fig. 1.

The annual cycle begins during the winter (w) and ends after summer (s). The population size (N) during the summer in given year (Ns_t) can be represented by N the previous winter (Nw_t) times per capita breeding output during the summer (b_t):

$$Ns_t = Nw_t b_t \tag{1}$$

Similarly, Nw_t can be represented by the product of N the previous summer at year $t-1$ (Ns_{t-1}) and survival rate during year winter ($1-d_t$):

$$Nw_t = Ns_{t-1}(1-d_t) \tag{2}$$

Expanding Nw_t in Eq. 1 gives:

$$Ns_t = Ns_{t-1}(1-d_t)(b_t) \tag{3}$$

Ns_t can, therefore, be determined through knowledge of b_t, d_t and Ns_{t-1}.

For simplicity, density-dependent breeding output and winter mortality at time t are represented as straight-line functions:

$$b_t = b_0 - b_1 Nw_t \tag{4}$$

$$d_t = d_0 + d_1 Ns_{t-1} \tag{5}$$

where d_0 and b_0 are the intercepts (per capita density-dependent rates as density approaches zero) and d_1 and b_1 are the slopes (strength of density-dependence: Sutherland 1996). Note that the shape of the functions

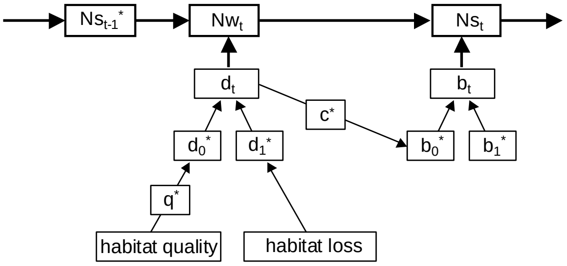

Fig. 1. Schematic diagram of the migratory population model, predicting the population size at Ns_t. Variables with asterisk require known values. The model can, therefore, be run without knowledge of winter population size (Nw_t) but the previous summers' population size (Ns_{t-1}) and the parameters of the winter (d_t) and summer (b_t) density-dependent functions must be determined. A change in the amount of winter habitat is reflected by a shift in the slope (d_1) of the winter density-dependent function. q determines how much of the habitat lost is of high quality and directly affects the intercept (d_0) of the winter mortality function (d_t). c is the carry-over effect resulting from loss of high quality winter habitat and directly affects the intercept (b_0) of the breeding output function (b_t). The model is run for successive years until equilibrium is reach (when $1/b_t = 1-d_t$ or $Ns_t = Ns_{t-1}$).

will depend on species-specific density-dependent relationships. The intersection between these functions is the equilibrium population size (E) and it is reached when $1/b_t = 1 - d_t$ or similarly when $Ns_t = Ns_{t-1}$ after successive iterations of the annual cycle.

Habitat loss and the 'seasonal compensation effect'

Habitat loss in a particular season is represented by a change in the slope of b_1 or d_1 of the function corresponding to that season (b_t or d_t, respectively), resulting in a subsequent decline in E (Fig. 2a). Sutherland (1996) showed that it is the relative strength of density dependence between winter (d_1) and summer (b_1) that will determine how populations are affected by habitat loss. For example, if habitat is lost on the wintering grounds and d_1 is stronger than b_1, the percentage population decline will approximate the percentage decline in habitat. If d_1 is weaker than b_1, population decline will be much less than the proportional decrease in winter habitat. Importantly, as long as there is density-dependence in the season following habitat loss, population decline will be proportionally less than the habitat lost in previous season.

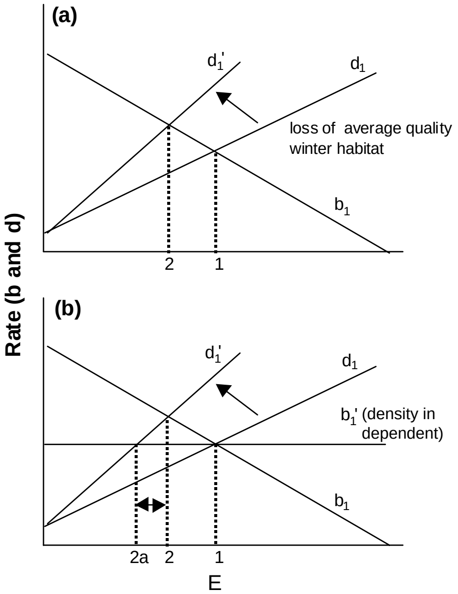

Fig. 2. (a) The effect of the loss of average quality winter habitat on equilibrium population size (E). The winter density-dependent mortality curve changes slope (d to d′) in relation to the percent habitat loss (Sutherland 1996). (b) A similar loss of winter habitat would result in a larger decrease in E if breeding output (b) was density-independent (straight line). The difference between "2" and "2a" is the 'seasonal compensation effect', a relative increase in population abundance from winter habitat loss due to density-dependent breeding output. A similar situation could occur from summer to winter. Note: in this figure (and Fig. 3), E is reached when $b = d$. In the model presented in the text, E is reached when $1/b = 1 - d$. Although, these generate different E values, the concepts presented in this figure (and Fig. 3) are still applicable to the model.

A 'seasonal compensation effect' occurs as a result of density-dependence acting in the season following negative effects (e.g. habitat loss) in the previous season. This results in a relatively higher E than if there was no density-dependence in the following season. For example, although loss of winter habitat reduces population size, the remaining individuals will be at a lower density and have a higher per capita breeding output the following season. As a result, a relatively higher E will, theoretically, be achieved. The magnitude of this effect can be seen in Fig. 2b. Consider a shift in d to d′ as a consequence of winter habitat loss. When there is density-dependent breeding output (negative slope), E declines from "1" to "2". Conversely, if b is density-independent (zero slope), E decreases from "1" to "2a" and population decline is directly proportional to the loss of winter habitat. The difference between "2" and "2a" is what I have termed the 'seasonal compensation effect'. As Sutherland (1996) has shown, its magnitude will depend on the relative strengths of density-dependence between the seasons.

Habitat quality

In the equilibrium model presented thus far, the mean value of habitat lost is considered average quality (as described in Sutherland 1996). In this section, I explore the consequences of losing a disproportional amount of either high or low quality habitat from an organism with an ideal despotic distribution. Compare these scenarios: two wintering populations, each consisting of half high quality and half low quality habitat. Population A loses half of its total winter habitat but all of it is low quality. Population B loses the same amount of habitat but all of it is high quality. An increase in the strength of the density-dependent effect (e.g. via crowding) would presumably occur in both scenarios as a consequence of a decrease in the amount of available habitat. As shown above, this can be reflected through an increase in d_1. Population B, however, now consists of only low quality habitat and should, therefore, have higher mortality rates at any given population size compared to Population A. This disproportionate loss of high quality habitat can be reflected through a change in the intercept (d_0) of the mortality function (Fig. 3a). The overall effect on E is additive in that both absolute habitat area is lost (reflected by an increase in d_1) as well as high quality habitat (reflected by an increase in d_0).

For the model, I assume that there are two types of winter habitats (high and low quality) that initially occur in equal proportions. d_0 is affected by a loss or gain in the amount of high quality habitat lost in relation to the overall amount of habitat lost. Therefore, I let a

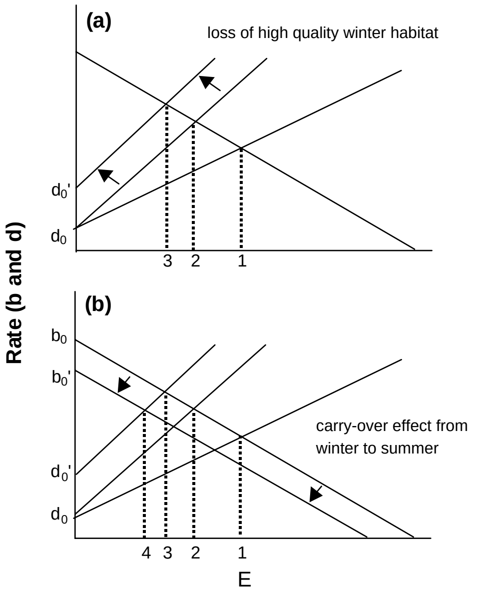

Fig. 3. (a) A loss of high quality winter habitat shifts the intercept of the winter mortality curve from d_0 to d_0', further decreasing equilibrium population size (E). The magnitude of this shift will depend on how much high quality habitat is lost in relation to the overall amount of habitat lost. (b) A carry-over effect from winter to summer would shift the intercept of the breeding output curve. A negative carry-over effect (decrease in b_0) will only occur if high quality winter is lost (change in d_0). The relationship between b_0 and d_0 will depend on the magnitude of the carry-over effect (‘c’ in model).

proportional change in d_0 (d_0 to d_0') equal a proportion shift in d_1 (d_1 to d_1') times q, the parameter that determines the effect of a disproportional loss of high quality habitat:

$$\frac{d_0' - d_0}{d_0'} = q\frac{d_1' - d_1}{d_1'} \tag{6}$$

Solving for d_0':

$$d_0' = \frac{d_0}{1 - q\dfrac{d_1' - d_1}{d_1'}} \tag{7}$$

where q = (p − 0.5). “p” is the percentage of high quality habitat lost in relation to the overall amount of habitat lost. For example, if the half of the total amount of habitat lost is high quality, p = 0.5 then q = 0. In this case, there is no change in d_0 as a result of winter habitat loss because the mean value of habitat lost is average quality (i.e. half high quality, half low quality). If three quarters of the total habitat lost on the wintering grounds is high quality, p = 0.75, q = 0.25, d_0 increases, further reducing E. Conversely, if only one-quarter of the habitat lost is high quality, p = 0.25, q = −0.25, and d_0 decreases.

Carry-over effects

Carry-over effects occur when individual success in one season is influenced by events in the previous season. For example, individuals occupying poor quality winter habitat may experience reduced reproductive success the following breeding season when compared to individuals occupying high quality winter habitat. This carry-over effect can be expressed at the population level. When a population experiences a loss of high quality habitat in the winter it has two results: (i) a decrease in winter population size (and subsequent reduction in E) as a result of habitat loss, and (ii) proportionally more individuals occupying poor quality habitat. Importantly, with a carry-over effect, the population will also experience a reduction in per capita breeding output the following season as a direct result of occupying (on average) poorer quality winter habitat. The decrease in b_t, therefore, is density- independent, such that at any given size the breeding population experiences a reduction in per capita breeding output.

This carry-over effect from winter to summer can be reflected though a shift in b_0 (Fig. 3b). The shift in b_0 is equal to a proportional change in d_0 times the carry-over effect parameter, c:

$$\frac{b_0' - b_0}{b_0'} = c\frac{d_0' - d_0}{d_0'} \tag{8}$$

Solving for b_0'

$$b_0' = \frac{b_0}{1 - c\dfrac{d_0' - d_0}{d_0'}} \tag{9}$$

where c varies from 0 to 1. 0 is no carry-over effect (b_0 does not shift due to a change in d_0) and 1 results in a proportionally equal change in b_0 due to a change in d_0.

Simulations

I ran two sets of simulations to investigate the influence of carry-over effects on equilibrium population size (E). A carry-over effect occurs because the quality of habitat occupied on the wintering grounds has an influence on individual reproductive success the following summer. At the population level, a larger proportion of high quality habitat results in a higher number of individuals over-wintering in this habitat type, translating to higher per capita reproductive success the following breeding season.

For all simulations, I used previous published parameters from oystercatchers, a long distance migratory shorebird. For a population of 2000 individuals, $d_1 = 0.00011$, $b_1 = 0.00005$ (Sutherland 1996). Therefore, I approximated $b_0 = 1.4$ and $d_0 = 0.001$, reasonable estimations given the values of per capita breeding output and per capita mortality at low densities for this species (Goss-Custard et al. 1995). Using these parameters, $E = 2180$. This value was very similar to the population size ($N = 2000$) used originally by Sutherland (1996) to estimate d_l and b_l.

To examine the influence of the carry-over effect, I simulated habitat loss on the wintering grounds, reflected by a change in the strength of density-dependence on the wintering grounds (d_l; see Appendix for calculations of percent loss of winter habitat). After habitat loss, the simulations were run until E was achieved (when $1/b_t = 1 - d_t$ or similarly when $Ns_t = Ns_{t-1}$).

Habitat loss and carry-over effects

First, I examined the impact of carry-over effects on E at levels of habitat loss between 0.1 and 75%. At the population-level, the carry-over effect impacts E when a disproportional amount of high quality habitat is lost in the winter (represented by q and resulting in a shift in d_0) and has negative consequences on the reproductive success (represented by c and resulting in a decrease in b_0) the following summer(s). I measured the relative contribution of c to overall decline in E by subtracting the decline in E with a carry-over effect from the decline in E without a carry-over effect then divided by the total decline.

Habitat quality and carry-over effects

Second, I examined the impact of losing different proportions of high quality winter habitat (represented by q) on E with and without a carry-over effect. Values of q ranged from -0.5 (all habitat lost is low quality) to 0 (loss of equal proportions of high and low quality) to 0.5 (all high quality). For each level of q, I then varied levels of total habitat loss from 0.1 to 50%. In all cases, $c = 0.5$. For comparison, I repeated this simulation but with no carry-over effect ($c = 0$).

Results

Habitat loss and carry-over effects

As winter habitat loss increased (0.1 to 75%), E decreased from an initial equilibrium value of 2180 (Fig. 4a). At all levels of habitat loss, E was lower when c was larger. For example, with zero carry-over effect ($c = 0$), half of the initial E was reached at 55% habitat loss. When $c = 0.6$, half the initial E occurred at 45% habitat loss; when $c = 1$, one-half of E occurred at 35% habitat loss. The decrease in E was also nonlinear; when $c = 1$, E declined more rapidly between 0.5 and 50% compared to when $c = 0$ (Fig. 4a).

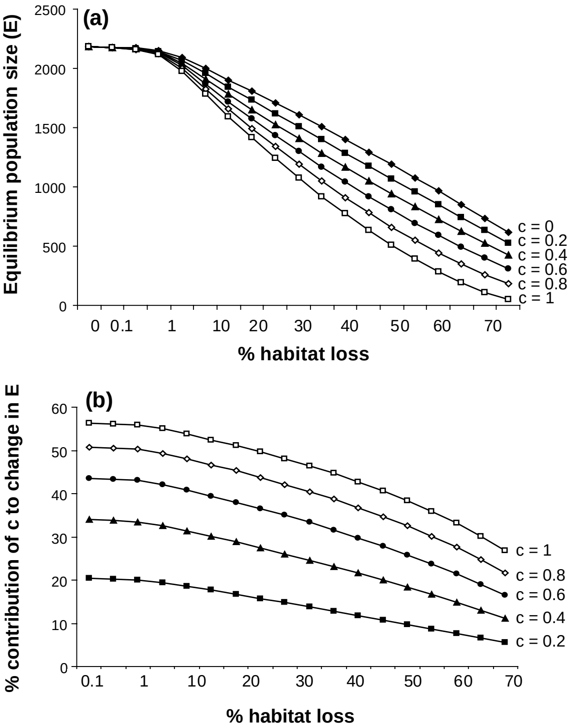

Fig. 4. (a) Equilibrium population size (E) in relation to habitat loss. Population size is based on Eq. 3, where $Ns_{(t-1)} = 2180$, $b_0 = 1.4$, $b_l = 0.00005$, $d_0 = 0.001$. Each line represents a different level of carry-over effect incorporated into the model. In all cases, $q = 0.5$, meaning that the habitat lost was high quality. (b) The percent decrease in E attributed to carry-over effects at different amounts of winter habitat loss. Each line represents a different level of carry-over effect. The y-axis is calculated by subtracting the decrease in E for a given level of carry-over effect ($c > 0$) from the decrease in E when there is no carry-over effect ($c = 0$), relative to the total decrease in E.

Although reductions in E were small at low levels of habitat loss, c contributed the greatest proportion to a decline in E at low levels of habitat loss (Fig. 4b). For example, the overall contribution of c to total population decline was over 50% when c was between 0.8 and 1 and absolute habitat loss was 1% or less.

Habitat quality and carry-over effects

When a carry-over effect was present ($c = 0.5$), E decreased as the proportion of high quality winter habitat lost increased (Fig. 5). In the absence of a carry-over effect ($c = 0$), the proportion of high quality habitat lost (q) had little influence on E. This was true even at high percentages of habitat loss. When a carry-over effect was present and the majority of habitat lost was low quality (negative q), q had a positive effect on E (Fig. 6a). In other words, E was higher relative to when $q = 0$. When the majority of habitat lost was high quality, (positive q), q had a negative effect on E

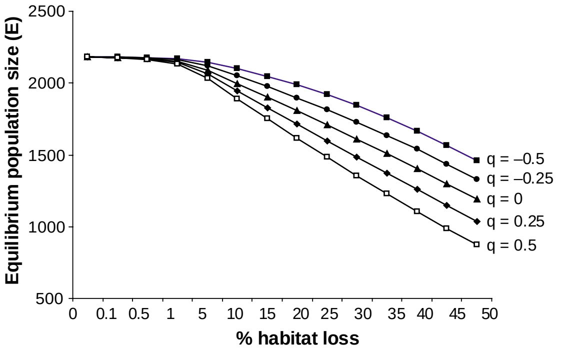

Fig. 5. (a) Equilibrium population size (E) in relation to habitats loss at different levels of q (lines). Population size is based on equation (3), where $Ns_{(t-1)} = 2180$, $b_0 = 1.4$, $b_1 = 0.00005$, $d_0 = 0.001$. For all levels, $c = 0.5$.

(additional decline relative to $q = 0$; Fig. 6a). The overall impact on E was larger when the majority of habitat lost on the wintering grounds was low quality (q was negative) because of the seasonal compensation effect (Discussion). When there was no carry-over effect ($c = 0$), different proportion of high quality habitat lost (q) had minimal impacts on E, either positive or negative (Fig. 6b; compare scale on y-axis to Fig. 6a).

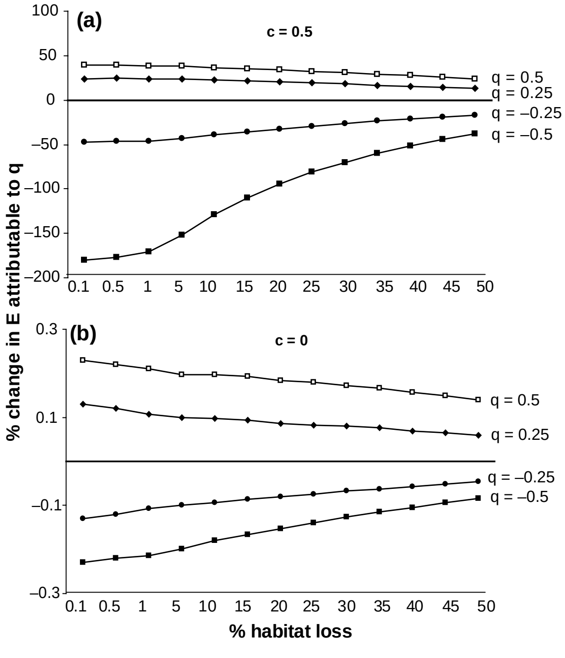

Fig. 6. Habitat quality and carry-over effects. (a) After habitat loss, the percent change of equilibrium population size (E) that can be attributed to q (reflecting the proportion of high quality habitat lost in relation to overall loss). Each line represents a different level of q, where a negative q values represent a greater proportion of low quality habitat loss than high quality. The y-axis is calculated by subtracting the decrease in E for a given value of q from the decrease in E when $q = 0$ (equal amounts of high and low quality habitat lost). (b) as in (a) but $c = 0$. Note the different scale of the y-axis compared to (a).

Discussion

I have shown that carry-over effects and habitat quality can be incorporated into a density-dependent equilibrium population model for migratory organisms (Fretwell 1972, Sutherland 1996). Habitat quality has been shown to have important effects on reproductive success, survival and physical condition both in summer (Holmes et al. 1996, Murphy 2001, Part 2001) and winter (Strong and Sherry 2000, Marra and Holmes 2001). The relative amounts of different quality habitat, therefore, should be taken into consideration when calculating absolute habitat loss. In the equilibrium model, b_0 and d_0 represent the breeding output and mortality rates as density approaches zero. The important characteristic of these parameters is that they are averaged over all habitat types. Therefore, changes in the proportion of different quality habitats will change the value of these intercepts. On the other hand, if habitat is lost but the proportion of different quality habitats remain the same, only the strength of density-dependence (represented by d_1 or b_1) will increase. The interpretation of these parameters represents a key fundamental concept that should be taken into account when considering population models of migratory organisms.

I have also shown that carry-over effects at the individual level can have potentially important implications for migratory population dynamics. Specifically, carry-over effects can magnify population declines when there is an increase in the proportion of individuals experiencing a negative carry-over effect. For example, when the proportion of individuals over-wintering in poor quality habitat increases, the per capita reproductive success of the population will decline the following season. This exacerbates population declines, which are already affected by increased mortality due to loss of habitat on the wintering grounds.

Equally as important, the model shows that carry-over effects can also have positive effects on population size. For example, in the model, when greater than half of the habitat lost is low quality (q is negative), a positive (and additive) effect on E occurs in the following way: first, as a result of low quality habitat loss, a larger proportion of individuals occupy high quality winter habitat, producing a positive carry-over effect on per capita breeding output the following season. Second, fewer individuals on the wintering grounds results in higher per capita breeding output from density-dependence the following season (i.e. the seasonal compensation effect). In this way, loss of low quality habitat may have minimal impacts on E (Fig. 6), particularly if carry-over effects are strong.

I made the following three model assumptions regarding the influence of carry-over effects at the population level. First, the carry-over effect does not interact with density on the breeding grounds. It is possible that carry-over effects may have their largest impact at high densities the following season. If this were the case, the carry-over effect (c) would increase the slope of b_1 (strength of density-dependence) instead of a causing a shift in b_0. Determining the relative impact between density-dependence factors and carry-over effects will be another important component to understanding population dynamics.

The second assumption is that changes in density on the wintering grounds do not influence the strength of the carry-over effect. If the majority of habitat lost on the wintering grounds is high quality, surviving individuals will presumably increase the density in low quality habitat. The second assumption would be violated if higher densities further increase the population-level carry-over effect (value of c) on reproduction during the breeding season. Conversely, if mostly low quality habitat is lost, densities may increase in higher quality habitat, decreasing the positive impacts of a carry-over effect. It will, therefore, be important to understand how density interacts with 'intrinsic' quality, particularly after a significant amount of habitat is lost.

Third, I assume that organisms show an ideal-despotic distribution, implying that there is an asymmetric distribution of fitness across different quality habitats. If organisms are distributed in an ideal-free fashion on the wintering grounds, a carry-over effect may have little influence on the per capita breeding success the following season if individuals are able to redistribute themselves over the landscape after habitat loss. All birds would have the same fitness during the winter, regardless of the quality of habitat that is lost. The carry-over effect, therefore, would not change per capita breeding success the following summer.

Until recently, carry-over effects have been overlooked in many migratory species (with the exception of waterfowl and geese), primarily because of the difficulty of tracking individuals from one season to the next. While only a few studies using mark–recapture have yielded a sufficient sample size to determine carry-over effects (Gill et al. 2001), new techniques such as stable isotope analysis, are providing cheaper and easier ways to track individuals year round (Marra et al. 1998, Norris et al. 2004). It seems reasonable to speculate that carry-over effects will be prominent in other migratory species. In particular, events that have negative but nonfatal effects on individuals will likely result in carry-over effects into the subsequent season. The scenario I have presented in this model is one example: after loss of high quality winter habitat, surviving individuals are forced into smaller areas of low quality, increasing density, and resulting in lower mean reproductive success for the population the following season. Species that show strong density-dependence as a result of crowding may be more susceptible to carry-over effects resulting from loss of habitat. In contrast, species that are strongly territorial (territories do not constrict as density increases), loss of habitat may only result in high mortality rates.

Carry-over effects, however, need not be associated with density-dependence the previous season. For example, North American passerines breeding in some fragmented habitats have been shown to experience high rates of brood parasitism by brown-headed cowbirds (*Molthus ater*; Robinson and Wilcove 1994, Robinson et al. 1995). Brood parasitism can not only result in lower reproductive success (Pease and Grzybowski 1995) but also increased feeding rates by adults (Winfree 1999). Higher feeding rates could compromise the physical condition of adults, lowering their ability to acquire high quality habitat the following winter.

In addition, the geographic connectivity of migratory populations (Webster et al. 2002) will influence how carry-over effects are expressed the following season. For example, populations may show strong geographic structuring on the wintering grounds but high dispersal rates (population mixing) on the breeding grounds. Loss of high quality habitat in one wintering area, therefore, may have negative consequences on the ability of those individuals to compete with other individuals (overwintering in different areas) for resources on the breeding grounds.

The specific mechanism of carry-over effects presented in this model (high quality winter habitat loss resulting in a decrease in reproductive success) may not be applicable to all systems. However, different types of carry-over effects, influencing various demographic parameters can be incorporated relatively easily into specific systems. For example, individuals may experience strong carry-over effects from an increase in brood parasitism or nest predation on the breeding grounds. In turn, this may decrease their ability to secure high quality habitat the following winter through a decrease in physical condition the preceding breeding season.

To predict changes in population size for migratory animals, it will be important to determine (i) the strength of density dependence in both seasons, and (ii) which demographic factors in which season produce strong carry-over effects. If carry-over effects are significant, they could magnify the effects of habitat loss by counteracting seasonal compensation effects in the following season, leading to further population declines.

Acknowledgements – Dan Haydon provided valuable insight during the initial stages of the project. I thank Laurene

Ratcliffe, Peter Marra and Bill Sutherland for many constructive comments on the manuscript. I am especially grateful to Mike Runge for enormously helpful reviews of the manuscript. The author was supported by the Smithsonian Institution, the National Science Foundation (Grant No. 0089565, P. P. Marra and T. W. Sherry), the Natural Sciences and Engineering Research Council of Canada (NSERC grant to L. M. Ratcliffe), and through scholarships from NSERC and the Ontario government.

References

Baillie, S. R., Sutherland, W. J., Freeman, S. R. et al. 2000. Consequences of large-scale processes for the conservation of bird populations. – J. Anim. Ecol. 37(S): 88–102.

Dolman, P. M. and Sutherland, W. J. 1994. The response of bird populations to habitat loss. – Ibis 137: S38–S46.

Durell, S. E. A. Le V. Dit., Goss-Custard, J. D. and Clarke, R. T. 1997. Differential response of migratory subpopulations to winter habitat loss. – J. Appl. Ecol. 34: 1155–1164.

Fretwell, S. D. 1972. Populations in a seasonal environment. – Princeton Univ. Press.

Gill, J. A., Norris, K., Potts, P. M. et al. 2001. The buffer effect and large-scale population regulation in migratory birds. – Science 412: 436–438.

Goss-Custard, J. D., Clarke, R. T., Briggs, K. B. et al. 1995. Population consequences of winter habitat loss in a migratory shorebird. I. Estimating model parameters. – J. Anim. Ecol. 32: 320–336.

Greenberg, R. and Marra, P. P. (eds) 2005. Birds of two worlds: the ecology and evolution of temperate-tropical migration systems. – In press, John Hopkins Univ. Press.

Hagan, J. M. and Johnston, D. W. (eds) 1992. Ecology and conservation of Neotropical migrant landbirds. – Smithsonian Inst. Press.

Holmes, R. T., Marra, P. P. and Sherry, T. W. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. – J. Anim. Ecol. 65: 183–195.

Keast, A. and Morton, E. S. (eds) 1980. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. – Smithsonian Inst. Press.

Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. – J. Avian Biol. 27: 164–170.

Marra, P. P. and Holmes, R. T. 2001. Consequences of dominance-mediated habitat segregation in a migrant passerine bird during the non-breeding season. – Auk 118: 92–104.

Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable carbon isotopes. – Science 282: 1884–1886.

Martin, T. E. and Finch, D. M. (eds) 1995. Ecology and management of Neotropical migratory birds. – Oxford Univ.

Murphy, M. T. 2001. Habitat-specific demography of a long-distance, neotropical migrant bird, the eastern kingbird. – Ecology 82: 1304–1318.

Newton, I. 2004. Population limitation in migratory birds. – Ibis 146: 197–226.

Norris, D. R., Marra, P. P., Kyser, T. K. et al. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. – Proc. R. Soc. B 271: 59–64.

Part, T. M. 2001. Experimental evidence of environmental effects on age-specific reproductive success: the importance of resource quality. – Proc. R. Soc. B 268: 2267–2271.

Pease, C. M. and Grzybowski, J. A. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. – Auk 112: 343–363.

Pettifor, R. A., Caldow, R. W. G, Rowcliffe, J. M. et al. 2000. Spatially explicit, individually-based models of the annual cycle of two migratory goose populations. – J. Appl. Ecol. 37 (S1): 103–135.

Robinson, S. K. and Wilcove, D. S. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. – Bird Cons. Intl. 4: 233–249.

Robinson, S. K., Thompson III, F. R., Donovan, T. M. et al. 1995. Regional forest fragmentation and the nesting success of migratory birds. – Science 267: 1987–1990.

Sherry, T. W. and Holmes, R. T. 1996. Winter habitat quality, population limitation, and conservation of neotropical nearctic migrant birds. – Ecology 77: 36–48.

Sillett, T. S., Holmes, R. T. and Sherry, T. W. 2000. Impacts of a global climate cycle on populations dynamics of a migratory songbird. – Science 288: 2040–2042.

Strong, A. M. and Sherry, T. W. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. – J. Anim. Ecol. 69: 883–895.

Sutherland, W. J. 1996. Predicting the consequences of habitat loss for migratory populations. – Proc. R. Soc. B 263: 1325–1327.

Webster, M. S., Marra, P. P., Haig, S. M. et al. 2002. Links between worlds: unraveling migratory connectivity. – Trends Ecol. Evol. 17: 76–83.

Winfree, R. 1999. Cuckoos, cowbirds and the persistence of brood parasitism. – Trends Ecol. Evol. 14: 338–343.

Zanette, L. 2000. Fragment size and the demography of an area-sensitive songbird. – J. Anim. Ecol. 69: 458–470.

Appendix

Calculation of habitat loss on the wintering grounds

I let percent habitat loss on the wintering grounds be reflected through an increase in the slope of d_1. To calculate the change in the slope of d_1 for a given level of habitat loss I used to following method. Expanding b_t and d_t in the original model equation:

$$Ns_t = Ns_{t-1}(1 - d_t)(b_t) \tag{3}$$

gives:

$$Ns_t = Ns_{t-1}(1 - (d_0 + d_1 Ns_{t-1})) \times \{b_0 - b_1(Ns_{t-1}(1 - (d_0 + d_1 Ns_{t-1})))\} \tag{10}$$

Since equilibrium is reached when $Ns_{t-1} = Ns_t$, I simplified Eq. 10 by letting both Ns_{t-1} and $Ns_t = E$:

$$E = E(1 - (d_0 + d_1 E))\{b_0 - b_1(E(1 - (d_0 + d_1 E)))\} \tag{11}$$

To calculate an increase in d_1 in relation to a percentage decrease in E, I first let the strength of density-dependence on the breeding grounds equal zero ($b_1 = 0$) to remove breeding ground effects on E. I, therefore, had to adjust the value of b_0 given that $b_1 = 0$. To do this, I used the original parameters from the wintering grounds ($d_0 = 0.001$, $d_1 = 0.00011$), letting $E = 2180$ and $b_1 = 0$ (zero density-dependence), then solved for b_0. For this case, $b_0 = 1.317$.

Using these values, I decreased E by a specific percent (for example: 50% of 2180 = 1090) and then solved for d_1 the following way:

Let post mortality population size be defined as:

$$P = E(1-(d_0-d_1E)) \tag{12}$$

Eq. 11 can, therefore, be rewritten as:

$$E = P(b_0-b_1P), \text{ or} \tag{13}$$

$$b_1P^2-b_0P+E=0 \tag{14}$$

Solving Eq. 14 for P:

$$P=\frac{b_0 \pm \sqrt{b_0^2-4b_1E}}{2b_1} \tag{15}$$

Combining Eq. 15 with Eq. 12:

$$E(1-(d_0-d_1E))=\frac{b_0 \pm \sqrt{b_0^2-4b_1E}}{2b_1} \tag{16}$$

Solving for d_1:

$$d_1=\frac{b_0+(d_0-1)(2b_1E) \pm \sqrt{b_0^2-4b_1E}}{-2b_1E^2} \tag{17}$$

Using this equation, when $E = 1090$ (50% decrease), $d_1 = 0.000220002$ (when $d_0 = 0.001$, $b_1 = 1.317$, $b_0 = 0$). I used this value of d_1 value to reflect 50% habitat loss.