

Optimal conservation planning for migratory animals: integrating demographic information across seasons

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Abstract

Conservation strategies for migratory animals are typically based on ad-hoc or simple ranking methods and focus on a single period of the annual cycle. We use a density-dependent population model to examine one-time land purchase strategies for a migratory population with a breeding and wintering grounds. Under equal rates of habitat loss, we show that it is optimal to invest more, but never solely, in the habitat with the higher density dependence to habitat cost ratio. When there are two habitats that vary in quality within a season, the best strategy is to invest only in one habitat. Whether to purchase high- or low-quality habitat depends on the general life history of the species and the ratio of habitat quality to habitat cost. When carry-over effects are incorporated, it is almost always optimal to invest in high-quality habitat during the season that produces the carry-over effect. We apply this model to a threatened warbler population and show the optimal strategy is to purchase more breeding than wintering habitat despite the fact that breeding habitat is over ten times more expensive. Our model provides a framework for developing year-round conservation strategies for migratory animals and has important implications for long-term planning and management.

Introduction

Billions of dollars are allocated each year toward the conservation of migratory animals (Migratory Bird Conservation Commission 2008). Although decisions on how to allocate these funds usually focus on a single period of the annual cycle (e.g., Robbins *et al.* 1992; Basili & Temple 1999; Dankel *et al.* 2008 but see Klaassen *et al.* 2008), both empirical (Bêty *et al.* 2003; Bearhop *et al.* 2004; Norris *et al.* 2004) and theoretical work (Fretwell 1972; Norris 2005; Norris & Taylor 2006) have shown that the factors that limit population abundance of migratory animals result from a combination of events that occur throughout the year. Thus, if predicting population size requires knowledge of how the effects of seasons interact, then conservation decisions, such as land acquisitions, should also be based on knowledge of the relationship between demographic parameters throughout the annual cycle (Martin *et al.* 2007; Klaassen *et al.* 2008).

Here, we use a simple two-season population model to optimize the population carrying capacity of a migratory species under the threat of habitat loss. The model is designed to predict how to allocate funds optimally to purchase breeding and wintering (nonbreeding) habitat given the relative strength of density dependence and habitat cost, differences in habitat quality within a season, carry-over effects (residual effects in one season that carry over to influence individual success in the following season), general life history, and total budget size. We apply our model to a threatened migratory warbler to demonstrate how optimal purchases can be estimated from population parameters and how these decisions may differ from current conservation actions.

Basic model structure

Following Sutherland (1996), we use a two-season migratory population with a per capita winter (nonbreeding) mortality function ($fw(N_t) = d + d'N_{t-1}$) and a per

capita reproductive (breeding) function ($fb(N_t) = b - b'N_{t-1}$) where N is population abundance, d and b are density-independent parameters (intrinsic habitat quality as the population approaches zero) for the wintering and breeding grounds, respectively, and d' and b' are density dependence parameters for the same seasons. We assume that d' and b' are affected by changes in habitat quantity (Sutherland 1996), while d and b are affected by changes in habitat quality (Norris 2005). The relative values of d and b can also represent species with either a K - (b close to d) or r -selected (higher b than d) life history. We also assume that there is a fixed budget to purchase habitat but that it is not adequate to purchase all available habitat. The change in population size N at time t , is given by

$$\Delta N_t = N_{t-1}[(b - b'N_{t-1}) - (d + d'N_{t-1})]. \quad (1)$$

This is equivalent to the discrete-time logistic growth equation (i.e., $\Delta N_t = rN(1 - N/K)$). As such, we can solve for carry-capacity, K :

$$K = \frac{b - d}{b' + d'}. \quad (2)$$

Using this model, we explore how to allocate resources optimally to maximize K for a population under three scenarios: when (1) habitat that is lost on either the breeding or wintering grounds is of average overall quality, (2) habitat lost on either the breeding or wintering grounds varies in both quantity and quality, (3) changes in the quality of habitat produce residual effects that carry over to influence demographic rates the following season.

Model 1: habitat loss of average overall quality

We assume that when habitat is lost the population will occupy the remainder of the habitat such that the new density, D_t , will equal the previous density, D_{t-1} , times the inverse of the proportion habitat remaining:

$$D_t = \frac{N_{t-1}}{L(h)} = D_{t-1} * \frac{1}{h} \quad (3)$$

where L represents the amount of habitat at $t-1$, and h represents the proportion of habitat remaining at $t-1$. Applying this to the density-dependent parameters (b' and d'), K can be written as

$$K = \frac{b - d}{b'/p + d'/q} \quad (4)$$

where p is the proportion of breeding habitat purchased and q is the proportion of wintering habitat purchased (both vary between 0 and 1).

Cost constraints

Let the cost of purchasing habitat during given season, C_i , equal the amount of habitat available, L_i (ha), times the cost per unit of habitat, P_i (dollars/ha), where $i = B$ (breeding) or W (wintering). The total budget, C_t , is assumed to be a fixed and is always less than the cost of purchasing either the entire wintering or breeding habitat. Thus, the optimal strategy will always entail spending the entire budget, such that

$C_t = (p)(C_B) + (q)(C_W)$. Dividing both C_B and C_W by C_t gives

$$1 = (p)(C_B^*) + (q)(C_W^*) \quad (5)$$

where C_B^* and C_W^* are the ratios of the costs needed to purchase all L_B and L_W in relation to the total budget, respectively.

Model analysis and results

Effect of density dependence and habitat cost on purchase decisions

The optimal proportion of habitat purchased depends on the relative costs and strength of density dependence between the breeding and wintering season. We derived the equations for the optimal proportion of breeding, p_{opt} , and wintering habitat, q_{opt} , and also for the optimal proportion of the budget to spend on breeding or wintering habitats (see Appendix).

When the relative strength of density dependence is equal to the relative cost ($b'/d' = C_B^*/C_W^*$), then the optimal strategy is to purchase equal proportions of habitat between seasons (points of intersection in Figure 1A). When $b'/d' < C_B^*/C_W^*$, then the optimal strategy is to purchase more wintering than breeding habitat (Figure 1A) because the cost-per-unit increase in the strength of density dependence is less expensive for wintering habitat. As the b' increases prior to a purchase decision, there is a sharp increase in p_{opt} and a sharp decrease in q_{opt} (Figure 1A). If $C_B^* = C_W^*$ but $b' \neq d'$, it is optimal to purchase more of the habitat with the stronger density dependence. If $b' = d'$ but $C_B^* \neq C_W^*$, it is optimal to purchase more of the habitat with the lower cost.

When the density dependence times the cost is equal between habitats ($b'C_B^* = d'C_W^*$), then the optimal strategy is to spend the budget evenly between the two habitats (points of intersection in Figure 1B). When $b'/d' < C_W^*/C_B^*$, then the optimal strategy is to invest a larger proportion of the budget in wintering habitat (Figure 1B). If $C_B^* = C_W^*$ but $b' \neq d'$, it is optimal to invest more of the budget in the habitat with the higher density dependent parameter and, if $b' = d'$ but $C_B^* \neq C_W^*$, it is optimal to

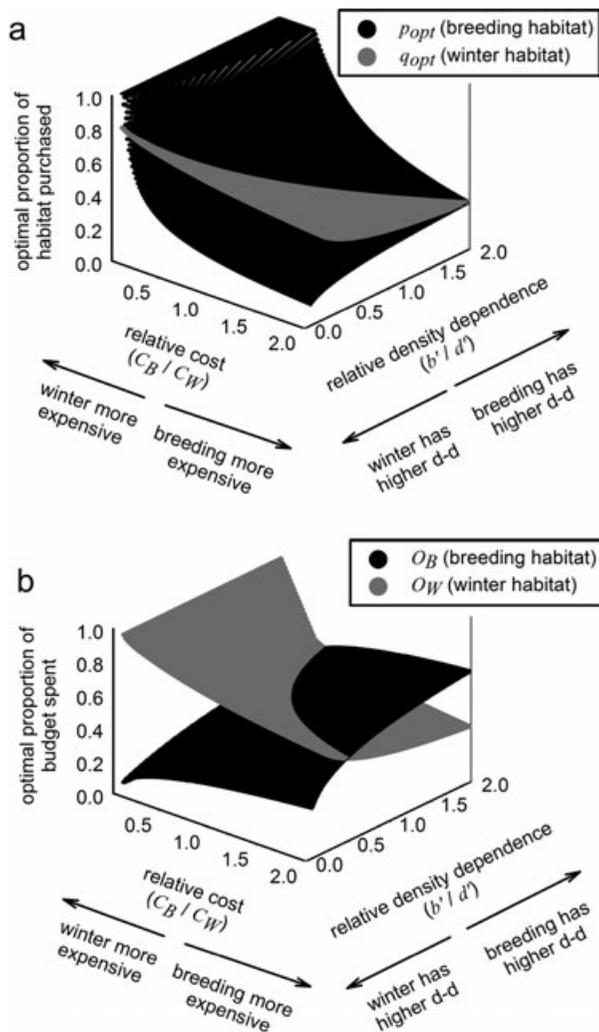


Figure 1. The optimal proportion of (a) breeding, p_{opt} (black), and wintering, q_{opt} (gray), habitat purchased, and (b) total budget spent on breeding, O_B (black), and wintering, O_W (gray), habitat in relation to the relative strength of density dependence (b'/d') and the relative cost (C_B/C_W) between the two seasons. For both panels, $C_W^* = 1.2$ and C_B^* varies, $d' = 0.00011$, b' varies, $b = 0.4$, and $d = 0.05$.

invest more of the budget in the habitat with the higher cost.

Effect of absolute habitat cost on purchase decisions

As the price of either habitat increases prior to the purchase (and the cost of the other habitat remains the same), the optimal strategy is to decrease the purchase of habitat in both seasons rather than just that the habitat that increased in price (Figure 1A; C_B^* varies while C_W^*

is fixed). The converse is also true: as habitat cost declines in one season, resources should be allocated to habitats in both seasons.

Model 2: habitat quality

We modify this model to include two quality habitats in one season, and assume an equal area within each habitat and a higher cost associated with the high-quality habitat, which creates a trade-off between purchasing quality versus quantity. A difference in habitat quality is represented by variation in the density-independent parameter (d_{high}, d_{low} for wintering, b_{high}, b_{low} for breeding). Thus, d and b are the weighted averages of these parameters. For example:

$$d = \frac{q_{low}(d_{low}) + q_{high}(d_{high})}{q_{low} + q_{high}} \tag{6}$$

A similar equation applies when in a two-quality breeding habitat model except, in this case, higher-quality habitat has a higher b value. Equations for K and the cost constraint can be easily modified from Equations (4) and (5) to include habitat quality (see Appendix).

Simulations

Because p_{opt} and q_{opt} cannot be solved analytically with multiple habitat qualities, we ran simulations to maximize K (see Appendix for equations used to calculate K and C_i). Three models were run: two quality wintering habitat and a single breeding habitat, two quality breeding habitat and a single wintering habitat, and two habitat qualities in both seasons (see Appendix for details). We used population estimates from Eurasian oystercatchers (*Haematopus ostralegus*; Sutherland 1996) and obtained approximate land cost values from the Migratory Bird Conservation Commission Report (2008).

Model analysis and results

Effect of relative density dependence and cost on purchase decisions

Consistent with model 1, the between-season purchase decisions are determined by the relative strength of density dependence (Figure 2A) and cost (Figure 2B) between the two habitats. However, within a season, the optimal strategy is to only invest in one type of habitat quality and this depends on (1) the relative density-independent values and costs of the habitats (Figure A1) and (2) the relative density-independent values between seasons (for the wintering quality purchase decisions; Figure 2C). These results are the same when there are

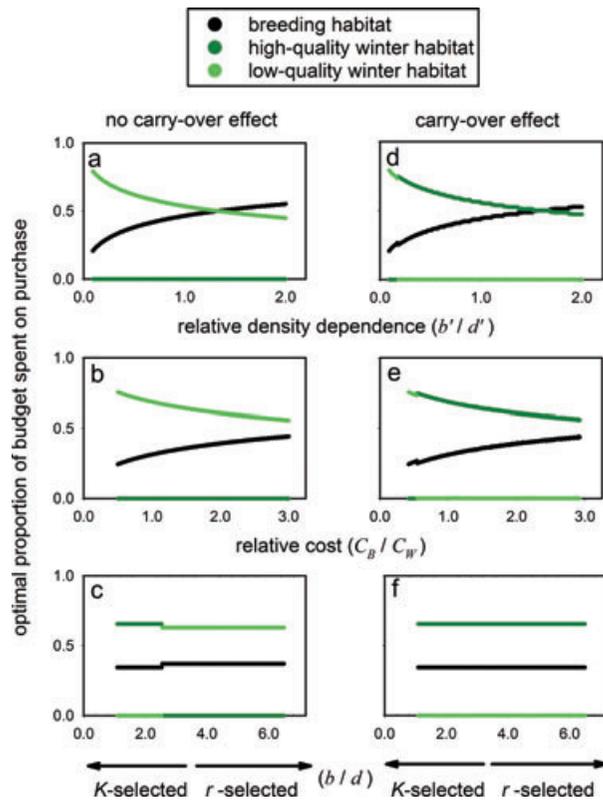


Figure 2. The optimal proportion of budget spent on high- and low-quality wintering habitat, total winter habitat, and total breeding habitat without (left-hand panels) and with (right-hand panels) carry-over effects incorporated into the model, in relation to the relative strength of density dependence between the breeding and wintering habitat (a and d), the relative cost of breeding to wintering habitat (b and e), and the ratio of mean breeding to wintering habitat quality (c and f). For (a) and (d), $C_B^* = 3.25$, b' varies, $b = 0.4$. For (b) and (e), C_B^* varies, $b' = 0.00005$, $b = 0.4$. For (c) and (f), $C_B^* = 3.25$, $b' = 0.00005$, and b varies. For (d), (e), and (f), $C_{high} = 0.05$. For all panels, $d_{high} = 0.05$, $d_{low} = 0.06$, $C_{W_{low}}^* = 2.15$, $C_{W_{high}}^* = 2.6$, $d' = 0.00011$. [Correction added after online publication 2 February 2010: In Figure 2, sections A4 and A5, the K and the r (for the selected species) were originally accidentally switched.]

two qualities on the breeding grounds (Figure A2), and when there are two habitat qualities in both seasons (Figure A3).

The effect of life history on optimal purchase decisions within a season

In *K*-selected species, the optimal strategy is to invest only in the high-quality wintering habitat (Figure 2C). However, in *r*-selected species, the optimal strategy is typically to focus resources on acquiring low-quality wintering habitat (Figure 2C). The *b* to *d* ratio does not influence the optimal purchase strategy when there are two different quality habitats on the breeding grounds (Figure A4).

This result also holds when there are two different quality habitats in both seasons (Figure A5).

Effect of relative cost and quality within a season

It is optimal to invest in high-quality wintering habitat when a higher *K* will result from the higher *b/d* ratio (associated with higher quality habitat) rather than the larger amounts of low-quality habitat that can be purchased at a relatively low price. These results also apply when there are two different habitat qualities on the breeding grounds (Figure A2) and two habitat qualities in both seasons (Figure A3).

Model 3: carry-over effects

We added a carry-over effect, *c*, into model 2, which indicates how the quality of habitat in one season influences the density independent parameter the following season (varies between 0 and 1; Norris 2005). We assigned a *c* value to the high-quality wintering habitat, c_{high} . Thus, *c* is determined by the proportion of high-quality wintering habitat purchased:

$$c = \frac{c_{high}(q_{high})}{q_{high} + q_{low}} \tag{7}$$

Equations for *K* and the cost constraints modified to include *c* are presented in the Appendix. Simulations for the optimization are the same as aforementioned.

Model analysis and results

With the addition of *c*, the optimal strategy switches from investing in low- to high-quality wintering habitat under a range of values for the other parameters (Figure 2D–F). The addition of *c* also removes any effect of life history on optimal decisions (Figure 2C and F). The optimal strategy depends on the relative strength of the carry-over effect (in the case from winter to summer, the ratio of *c/b*). When the relative strength of the carry-over effect is less than 0.05, there is little or no change in the quality purchased. Past this threshold, it becomes optimal to invest in the high-quality habitat (Figure A6). However, any further increase in the relative strength of carry-over effect has little or no effect on the proportions of habitat purchased (Figure A6). Changing the optimal purchase from low- to high-quality habitat is inversely related to the ratios of density dependence (*b'/d'*) and cost (C_B/C_W).

Application of the model

We show how our model can be applied to estimate the optimal amount of breeding and wintering habitat for

the hooded warbler (*Wilsonia citrina*), a 10 g migratory passerine that winters from east-central Mexico to Belize (Ogden & Stutchbury 1994). Hooded warblers are listed as “threatened” under the Canada Species at Risk Act (COSEWIC 2000) with the only Canadian breeding population located in southwestern Ontario. We used habitat quality and density-dependent estimates from published studies on this species and a closely related species (black-throated blue warbler *Dendroica caerulescens*; see Appendix and Table A1). We calculated the total habitat area in Ontario based on the Breeding Bird Atlas (Badzinski 2007) and assumed an equal area on the wintering grounds. In June 2009, the Nature Conservancy of Canada purchased 29 ha of Carolinian forest in Happy Valley for an estimated US\$300,000 (based on our property cost estimates) that was partially directed towards protecting hooded warblers. In Belize, the Runaway Creek Nature Reserve (2500 ha), in which hooded warblers are a common wintering migrant, is currently for sale for US\$2 million (Vista Real Estate 2009). Based on these estimates, our model shows that the optimal strategy is to purchase 1.85 times more breeding than wintering habitat (see Appendix for calculations). Assuming a total budget of US\$2.3 Million (the combined cost of these two purchases), the optimal strategy is to purchase approximately 210 ha of breeding habitat in Ontario and approximately 112 ha of habitat in Belize. This would result in a K of 55 individuals, which is higher compared to either purchasing only 29 ha on the breeding grounds ($K = 0$) or purchasing both this habitat and the 2500 ha on the wintering grounds ($K = 8$; see Appendix for calculations). Furthermore, when multiple habitat qualities are incorporated (Table A2), the optimal strategy is to purchase 164 ha of high-quality breeding habitat and 95 ha of high-quality wintering habitat, a strategy that leads to an even higher K (~65 individuals; see Appendix).

Discussion

We demonstrate how a two-season population model can be used to optimize the proportion of land purchased for a migratory animal using multiple habitats over the course of an annual cycle. Given equal rates of habitat loss, the optimal conservation strategy is to invest proportionally more during the season with the higher density dependence to land cost ratio because this is the period of the annual cycle that provides a larger return on investment (per dollar value relative to carrying capacity). However, the optimal strategy almost never results in investing solely in a single season. Multi-season investment is required because any increases in carry capacity in one season have to be matched by investments in other peri-

ods of the migratory cycle. Simultaneous investment has important implications for long-term planning and management because many conservation efforts for species under threat are focused on the period of the annual cycle that is believed to be the most limiting (e.g., Robbins *et al.* 1992; Basili & Temple 1999; Dankel *et al.* 2008).

When differences in habitat quality within a season are incorporated, we find that the between-season optimal purchase decisions are similar to the single-quality habitat model. However, within a season, the optimal strategy is to invest only in one type of habitat quality and any investment in the other habitat will lead to a sub-optimal population size. Of course, this result applies when limited funding precludes purchasing both habitat types and does not address how the long-term persistence might be influenced by these decisions.

The life history of the species also has important implications for optimal purchase designs. For K -selected species, it is optimal to invest primarily in high-quality habitat on the wintering grounds. Because K -selected species reproduce at a relatively low rate, the quantity of habitat is less important than the quality of habitat to maximize K . Conversely, for r -selected species, it is optimal to invest primarily in cheaper, low-quality winter habitat because a higher reproductive rate puts a premium on habitat quantity to maximize K .

When carry-over effects are incorporated, the optimal strategy is almost always to invest in higher quality habitat during the season that produced the carry-over effect. Surprisingly, this occurred even when the strength of the carry-over was minimal: when c was 0.1 (a unit change in habitat quality in one season influences habitat quality the following season by 10%), the optimal investment switched from investing in low- to high-quality habitat.

We also show how our model can be used to maximize the carrying capacity for a species currently listed as threatened in Canada. We found that the optimal strategy for hooded warblers is to spend a relatively high proportion on breeding habitat because the ratio between b'/d' is higher than the ratio of C_B^*/C_W^* , even though breeding habitat is estimated to be 12 times more expensive. Optimal purchase strategies will strongly depend on the relative population parameters between the breeding and wintering habitats and it is likely that current conservation efforts, whether focused solely on breeding habitat or biased toward purchasing cheaper wintering habitat, are not optimal strategies for protecting species.

Our framework can be applied to a variety of other scenarios that appear to focus on conservation in one period of the migratory cycle. For example, in 1986 the Mexican government purchased five habitat patches in Transvolcanic Mountain Range to conserve the overwintering sites of the Monarch butterfly (*Danaus plexippus*;

Bojórquez-Tapia *et al.* 2003) with no systematic conservation actions that paralleled this initiative on the breeding range. Similarly, in 1960; the American government protected 3.6 million ha of breeding habitat in Alaska (now known as the Arctic National Wildlife Refuge) that was primarily aimed at conserving the migratory Porcupine caribou herd (*Rangifer tarandus granti*; CRS 2002) and, in 1980, these lands were expanded by an additional 3.7 million ha (CRS 2002) with no plans to invest in non-breeding habitats south of the refuge.

The concept of optimizing population size over multiple seasons given a limited set of resources can also be applied to a wide range of factors that influence population abundance other than habitat loss. For example, changes in predation and variation in climate or food supply can be represented by shifts in d or b or shifts in the strength of density independence. The p_{opt} and q_{opt} optimization equations can be used in situations where managers wish to analyze the consequences of variation in cost parameters. For example, to examine the consequences of an increase in the cost of breeding habitat, one can increase the value of C_B in Equations (A1) and (A2) to calculate the change in the optimal proportion of breeding and wintering habitat purchased.

Our model demonstrates that developing effective conservation plans will require accurate estimates of density dependence, habitat quality, and the costs of performing conservation actions at multiple stages of the migratory cycle. The absence of such information will make it difficult to allocate funding effectively for protecting migratory populations (Martin *et al.* 2007) and can result in some populations continuing to decline, despite the fact that positive measures are being taken to protect their habitats.

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References

- Badzinski, D.S. (2007) Hooded Warbler. Pages 524–525 in M.D. Cadman, D.A. Sutherland, G.G. Beck, D. Lepage, A.R. Couturier, editors. *Atlas of the breeding birds of Ontario 2001–2005*. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, Ontario Nature, Toronto.
- Basili, G.D., Temple S.A. (1999) Dickcissels and crop damage in Venezuela: defining the problem with ecological models. *Ecology* **9**, 732–739.
- Bearhop, S., Hilton G.M., Votier S.C., Waldron S. (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *P Roy Soc Lond B Bio* **271**, S215–S218.
- Bêty, J., Gauthier G., Giroux J.-F. (2003) Body condition, migration and timing of reproduction in Snow Geese, a test of the condition-dependent model of optimal clutch size. *Am Nat* **162**, 110–121.
- Bisson, I.A., Stutchbury B.J.M. (2000) Nesting success and nest-site selection by a neotropical migrant in a fragmented landscape. *Can J Zool* **78**, 858–863.
- Bojórquez-Tapia, L.A., Brower L.P., Castilleja G. *et al.* (2003) Mapping expert knowledge: redesigning the monarch butterfly biosphere reserve. *Conserv Biol* **17**, 367–379.
- Committee on the Status of Endangered Wildlife in Canada. (2000) COSEWIC assessment and update status report on the Hooded Warbler *Wilsonia citrina* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.
- Congressional Research Service. (2002) CRS Report RL31278, Arctic National Wildlife Refuge: Background and Issues, LC, 1–119.
- Dankel, D.J., Skagen D.W., Ulltang O. (2008) Fisheries management in practice: review of 13 commercially important fish stocks. *Rev Fish Biol Fisher* **18**, 201–233.
- Fretwell, S.D. (1972) *Populations in a seasonal environment*. Princeton University Press, Princeton.
- Klaassen, M., Bauer S., Madsen J., Possingham H. (2008) Optimal management of a goose flyway: migrant management at minimum cost. *J Appl Ecol* **45**, 1446–1452.
- Martin, T.G., Chades I., Arcese P., Marra P.P., Possingham H.P., Norris, D.R. (2007) Optimal conservation of migratory species. *PLoS ONE* **2**, 1–5.
- Migratory Bird Conservation Commission. (2008) 2007 Annual Report-Migratory Bird Conservation Commission, 1–50.
- Norris, D.R. (2005) Carry-over effects and habitat quality in migratory populations. *Oikos* **109**, 178–186.
- Norris, D.R., Taylor C.M. (2006) Predicting the consequences of carry-over effects for migratory populations. *Biol Lett* **2**, 148–151.
- Norris, D.R., Marra P.P., Kyser T.K., Sherry T.W., Ratcliffe L.M. (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *P Roy Soc B-Biol Sci* **271**, 59–64.
- Ogden, L.J., Stutchbury B.J. (1994) Hooded Warbler (*Wilsonia citrina*) in A. Poole, F. Gill, editors. *The Birds of North America*. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, DC.
- Robbins, C.S., Fitzpatrick J.W., Hamel P.B. (1992) A warbler in trouble: *Dendroica cerulea*. Pages 549–562 in J.M. Hagan, D.W. Johnston, editors. *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.

Sillett, T.S., Holmes R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* **71**, 296–308.

Sillett, S.T., Rodenhouse N.L., Holmes R.T. (2004) Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* **85**, 2467–2477.

Sutherland, W.J. (1996). Predicting the consequences of habitat loss for migratory populations. *P Roy Soc B-Biol Sci* **263**, 1325–1327.

Vista Real Estate (2009) Property detail: Runaway Creek Wildlife Reserve. Available from: <http://www.belizerealestate.bz/index.php?action=listingview&listingID=255>. Accessed 29 October 2009.

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Appendix

Model 1: Habitat loss of average overall quality

Model analysis and results

(a) Effect of density dependence and habitat cost on purchase decisions

We derived the equations for the optimal proportion of breeding, p_{opt} , and wintering habitat, q_{opt} , by substituting Equation (5) into Equation (4), taking the derivative with respect to p (or q), setting the equation to zero and then solving for p (or q). Substituting the solutions into the second derivative of K with respect to p (or q) shows that so long as $b > d$, then

$$p_{opt} = \frac{\sqrt{b'}}{(\sqrt{C_B^*})(\sqrt{b'}) + (\sqrt{d'}) + (\sqrt{C_W^*})} \quad (A1)$$

and

$$q_{opt} = \frac{\sqrt{d'}}{(\sqrt{C_W^*})(\sqrt{d'}) + (\sqrt{b'}) + (\sqrt{C_B^*})} \quad (A2)$$

Thus,

$$\frac{p_{opt}}{q_{opt}} = \frac{\sqrt{b'}\sqrt{C_W^*}}{\sqrt{d'}\sqrt{C_B^*}} \quad (A3)$$

In terms of the available budget, the optimal proportion to spend on breeding habitat is

$$O_B = \frac{\sqrt{b'}(\sqrt{C_B^*})}{(\sqrt{b'}) + (\sqrt{d'}) + (\sqrt{C_W^*})} \quad (A4)$$

and for wintering habitat is

$$O_W = \frac{\sqrt{d'}(\sqrt{C_W^*})}{(\sqrt{d'}) + (\sqrt{b'}) + (\sqrt{C_B^*})} \quad (A5)$$

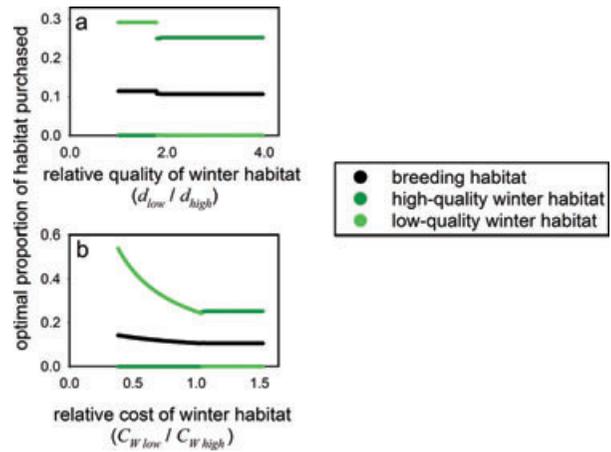


Figure A1. The optimal proportion of breeding habitat and low- and high-quality wintering habitat purchased in relation to the relative (a) intrinsic quality (d_{low}/d_{high}) and (b) cost ($C_{W_{low}}^*/C_{W_{high}}^*$) of the two different wintering habitats. For (a), d_{low} varies and $C_{W_{low}}^* = 2.15$. For (b), $d_{low} = 0.06$ and $C_{W_{low}}^*$ varies. For both panels, $C_{W_{high}}^* = 2.6$, $C_B^* = 3.25$, $b' = 0.00005$ and $d' = 0.00011$, $b = 0.4$, $d_{high} = 0.05$ and $C_{B_{low}}^* = 1.40$.

Model 2: Habitat quality

When there are two habitat qualities in the wintering season, the value of q is the average of the two qualities purchased:

$$q = \frac{q_{high} + q_{low}}{2} \quad (A6)$$

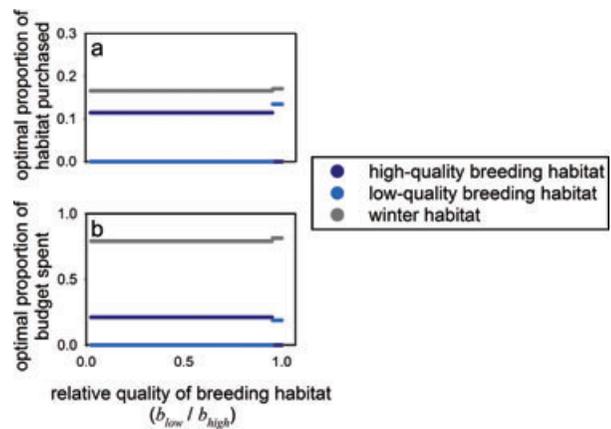


Figure A2. The optimal proportion of (a) low- and high-quality breeding habitat and total wintering habitat purchased and (b) proportion of the budget spent on the low and quality breeding habitat and total wintering habitat in relation to the relative intrinsic quality of the two different breeding habitats (b_{low}/b_{high}). For both panels, $C_{B_{high}}^* = 1.85$, $C_{B_{low}}^* = 1.40$, and $C_W^* = 4.75$. $b' = 0.00005$ and $d' = 0.00011$, $b_{high} = 0.4$, b_{low} varies, and $d = 0.05$.

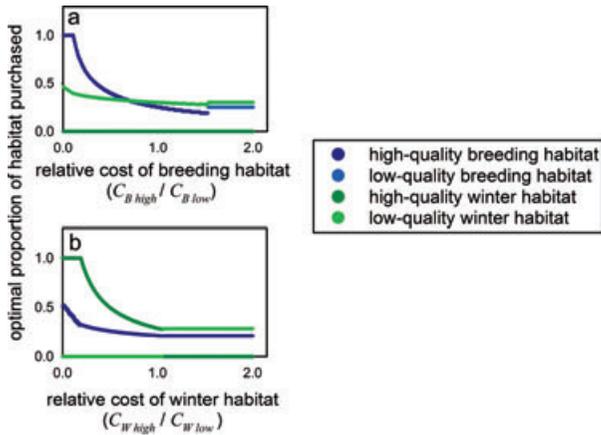


Figure A3. The optimal proportion of low- and high-quality habitat purchased for both breeding and wintering habitat in relation to the relative cost of (a) the two different breeding habitats ($C_{B_{high}} / C_{B_{low}}$) and (b) the two different wintering habitats ($C_{W_{high}} / C_{W_{low}}$). For (a), $C_{W_{low}}^*$ varies and $C_{W_{high}}^* = 2.15$. For (b), $C_{B_{low}}^* = 1.4$ and $C_{W_{low}}^*$ varies. For both panels, $C_{B_{high}}^* = 1.85$, and $C_{W_{high}}^* = 2.6$, b' varies, $d' = 0.00011$, $b_{high} = 0.4$, $b_{low} = 0.35$, $d_{high} = 0.05$, $d_{low} = 0.06$.

K can be modified to include two habitat qualities in the wintering season, by substituting Equations (6) and (A6) into Equation (4):

$$K = \frac{b - (q_{low}(d_{low}) + q_{high}(d_{high})) / (q_{low} + q_{high})}{(b'/p) + (2d' / (q_{high} + q_{low}))} \quad (A7)$$

and Equation (5) for the cost constraint can also be modified to include a two-quality wintering habitat:

$$1 = (p)(C_B^*) + (q_{low})(C_{W_{low}}^*) + (q_{high})(C_{W_{high}}^*). \quad (A8)$$

where C_B^* , $C_{W_{low}}^*$, and $C_{W_{high}}^*$ are the ratios of the costs to purchase all of the breeding and low and high-quality wintering habitat to the total budget. Similar equations apply when there are two different quality breeding habi-

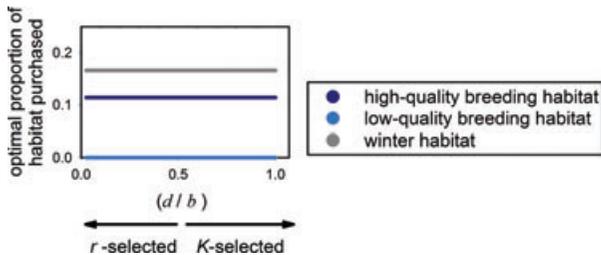


Figure A4. The optimal proportion of low- and high-quality breeding and average wintering habitat in relation to the ratio of mean wintering to breeding habitat quality. $C_{B_{high}}^* = 1.85$, $C_{B_{low}}^* = 1.40$, and $C_W^* = 4.75$. $b' = 0.00005$ and $d' = 0.00011$, $b_{high} = 0.4$, b_{low} varies, and $d = 0.05$.

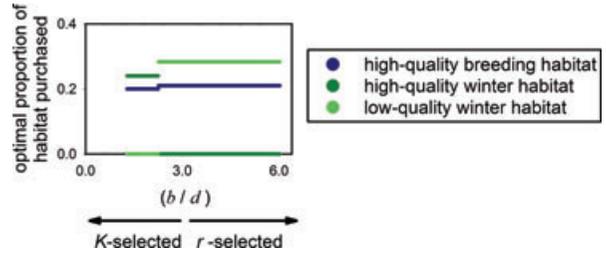


Figure A5. The optimal proportion of low- and high-quality habitat for both breeding and wintering habitat in relation to the ratio of mean breeding to wintering density dependence. $C_{B_{high}}^* = 1.85$, $C_{B_{low}}^* = 1.40$, and $C_{W_{high}}^* = 2.6$, $C_{W_{low}}^* = 2.15$. b' varies, $d' = 0.00011$, b_{high} and b_{low} vary, $d_{high} = 0.05$ and $d_{low} = 0.06$.

tats, except, in this case, higher quality habitat has a higher b value.

Simulations

For a given set of parameter values (b' , d' , b , d , C_B^* , and C_W^* for the single quality habitats, $C_{B_{high}}^*$, $C_{B_{low}}^*$, $C_{W_{high}}^*$, and $C_{W_{low}}^*$ for the two quality habitats), we varied the amount of each habitat and/or habitat quality purchased between 0 and 1 in increments of 0.01 and found the strategy that resulted in the highest K and also met the constraint of being less than or equal to G_r . All simulations were run using PELLE C (version 5.0: Pelle Orinius, 2008).

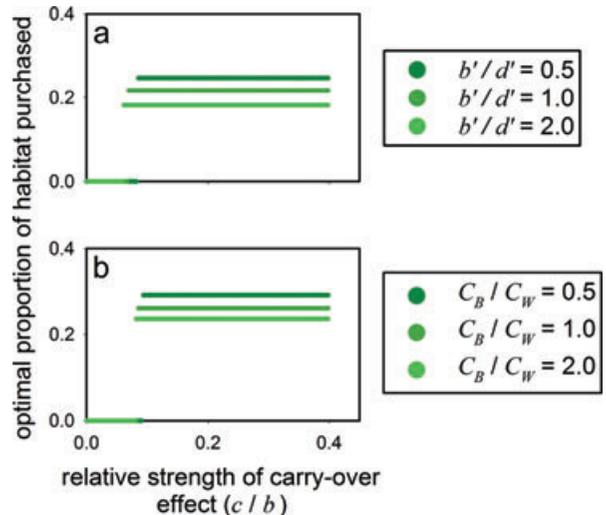


Figure A6. The optimal proportion of high-quality wintering habitat in relation to relative strength of carry-over effect and (a) the relative strength of density dependence between the breeding and wintering habitat, and (b) the relative cost of breeding habitat. For (a), $C_B^* = 3.25$, b' varies. For (b), C_B^* varies, $b' = 0.00005$. For all panels, $b = 0.4$, $d_{high} = 0.05$, $d_{low} = 0.06$, $C_{W_{low}}^* = 2.15$, $C_{W_{high}}^* = 2.6$. $d' = 0.00011$ and c varies.

Model 3: Carry-over effects

Because the value of b is increased by c , K , can be modified to

$$K = \frac{b(1+c) - \frac{q_{low}(d_{low}) + q_{high}(d_{high})}{q_{low} + q_{high}}}{\frac{b'}{p} + \frac{2d'}{q_{high} + q_{low}}} \quad (A9)$$

and Equation (5) for the cost constraint can also be modified in the following way:

$$1 = (p)(C_B^*) + (q_{low})(C_{W_{low}}^*) + (q_{high})(C_{W_{high}}^*). \quad (A10)$$

where C_B^* , $C_{W_{low}}^*$, and $C_{W_{high}}^*$ are the ratios of the costs to purchase all of the breeding and low and high-quality wintering habitat to the total budget. Similar equations apply when there are two different quality breeding habitats and the carry-over effect influences the wintering habitat.

Application of the model

Parameter estimates

We estimated b from the average number of Hooded warbler fledglings per female produced in southern Ontario (2.6 per pair/2 = 1.3; Bisson and Stutchbury 2000). We estimated the value of b' from experimental removals of breeding Black-throated blue warblers (*Dendroica caerulescens*; Sillet et al. 2004), a warbler species with a similar life history and breeding habitat. At low density, Sillet et al. (2004) found that breeding pairs fledged an average of 5.4 young at an average density of 0.353 (1 breeding pair per 5.7 ha). At high density, pairs fledged 3.6 young at an average density of 0.658 (1 breeding pair per 3.1 ha). The slope of the line (b') between the points is

$$b' = \frac{2.83 - 1.52}{0.353 - 0.658}$$

$$= -2.915(\text{fledglings/individual})/(\text{individual/ha}).$$

Because this value represents the density for the entire population per single hectare, we divided this by the total habitat size available so that it will be the measurement of density dependence for the entire habitat.

$$b' = \frac{2.915}{L_B}.$$

Therefore, if the breeding habitat size were 100 ha (for example), there would have to be an increase of 100 individuals in the population for the number of fledglings to decrease by 2.915 per individual.

The value of wintering mortality, d , was derived from the survival estimates of Black-throated blue warblers (Sillet and Holmes 2002). We took the two estimates of

survival during fall and winter migration (~0.73 each) and the probability of survival during the wintering period (0.93) to get a probability of survival for the entire nonbreeding period:

$$\text{Annual probability of survival} = 0.73 * 0.73 * 0.93 = 0.5.$$

However, because d is the probability of mortality then $d = (1 - \text{probability survival})$:

$$d = 1 - 0.5 = 0.5.$$

The average wintering survival probability for Black-throated blue warblers is 0.93 and the average density is 16 ± 3.8 birds per 5 ha plot (Sillet and Holmes 2002). To estimate the slope of the density dependence (d'), we took the survival probabilities \pm standard deviation (0.05) from the mean and densities \pm standard deviation (3.8) from the mean:

$$d' = \frac{0.12 - 0.02}{3.96 - 2.44} = 0.066.$$

However, this value also represents the density for the entire population per single ha. Therefore, we divided this value by the total habitat size available (in ha) so that it will be the measurement of density dependence for the entire habitat.

$$d' = \frac{0.066}{L_W}.$$

Optimal proportion calculations

Using Equation (A1) and parameter estimates in Table A1, the optimal proportion of breeding habitat can be calculated as

$$p_{opt} = \frac{\sqrt{1.54 \times 10^{-6}}}{\sqrt{8736.36((\sqrt{8736.36} * \sqrt{1.54 \times 10^{-6}}) + (\sqrt{673.93} * \sqrt{3.48 \times 10^{-8}}))}} = 0.00011 \cong 207.67\text{ha}$$

and the optimal proportion of wintering habitat can be calculated using Equation (A2):

$$q_{opt} = \frac{\sqrt{3.48 \times 10^{-8}}}{\sqrt{673.93((\sqrt{673.93} * \sqrt{3.48 \times 10^{-8}}) + (\sqrt{8736.36} * \sqrt{1.54 \times 10^{-6}}))}} = 0.00006 \cong 112.34\text{ha}.$$

By substituting these values into Equation (4), the resulting carrying capacity is

$$K = \frac{1.3 - 0.50}{\frac{1.54 \times 10^{-6}}{0.00011} + \frac{3.48 \times 10^{-8}}{0.00006}} \cong 55.$$

A strategy to purchase 29 ha of Carolinian forest in Southern Ontario, and 0 ha in Belize would yield the

Table A1. The parameter estimates used to model the optimal habitat purchase strategy for the hooded warbler and the source of these estimates

Parameter	Value	Source
b	1.3	Bisson & Stutchbury (2000)
d	0.5	Sillet & Holmes (2002)
b'	$\frac{2.915}{L_B}$	Estimated from Sillet et al. (2004) [†]
d'	$\frac{0.066}{L_W}$	Estimated from Sillet and Holmes (2002) [†]
L_B	1,890,000	Estimated from Atlas of the Breeding Birds of Ontario (2001)–(2005) [‡]
L_W	1,890,000	Assumed to be equal to breeding habitat
C_B^*	$\frac{10,667.77(L_B)}{\text{Budget}}$	Estimated from Carolinian Forest Lot purchase prices [§]
C_W^*	$\frac{823.68(L_W)}{\text{Budget}}$	Current price to purchase the Runaway Creek Nature Reserve

* Calculated by taking the difference in number of fledglings between the densities and dividing by the difference in density.

† Calculated by taking the difference in probability of survival between the densities and dividing by the difference in density.

‡ Estimated the potential habitat of the Hooded Warbler by creating a perimeter around the confirmed locations and measuring the area of the enclosed habitat.

§ Calculated by finding Carolinian forest lots for sale, and calculating a weighed-average of the costs per ha.

following p and q values:

$$p = \frac{29}{1890000} = 0.000015$$

$$q = \frac{0}{1890000} = 0.$$

By substituting these values into Equation (4), the resulting K is

$$K = \frac{1.3 - 0.50}{\frac{1.54 \times 10^{-6}}{0.000015} + \frac{3.48 \times 10^{-8}}{0}} = 0.$$

A strategy to purchase 29 ha of Carolinian forest in Southern Ontario, and 2,500 ha in Belize would yield the

Table A2. The parameter estimates used to incorporate multiple habitat qualities and determine the optimal proportion of high and low-quality breeding and wintering habitat in the example application

Parameter	Value	Source
b_{high}	1.65	Bisson & Stutchbury (2000) [*]
b_{low}	0.95	Bisson & Stutchbury (2000) [†]
d_{high}	0.45	Sillet & Holmes (2002) [‡]
d_{low}	0.55	Sillet & Holmes (2002) [§]
b'	$\frac{2.915}{(L_{B_{\text{high}}} + L_{B_{\text{low}}})}$	Estimated from Sillet et al. (2004)
d'	$\frac{0.0658}{(L_{W_{\text{high}}} + L_{W_{\text{low}}})}$	Estimated from Sillet & Holmes (2002)
$L_{B_{\text{high}}}, L_{B_{\text{low}}}, L_{W_{\text{high}}}, L_{W_{\text{low}}}$	945,000	Assumed to be equal to half of the available breeding/wintering habitat
$C_{B_{\text{high}}}^*$	$\frac{13,552.55(L_{B_{\text{high}}})}{\text{Budget}}$	Estimated from Carolinian forest lot purchase prices
$C_{B_{\text{low}}}^*$	$\frac{7,803(L_{B_{\text{low}}})}{\text{Budget}}$	Estimated from Carolinian forest lot purchase prices
$C_{W_{\text{high}}}^*$	$\frac{906(L_{W_{\text{high}}})}{\text{Budget}}$	Current price to purchase the Runaway Creek Nature Reserve [¶]
$C_{W_{\text{low}}}^*$	$\frac{741(L_{B_{\text{low}}})}{\text{Budget}}$	Current price to purchase the Runaway Creek Nature Reserve [¶]

* Calculated by taking the mean number of fledglings and adding 0.5 standard deviations.

† Calculated by taking the mean number of fledglings and subtracting 0.5 standard deviations.

‡ Calculated by taking the mean mortality probability and subtracting 0.5 standard deviations.

§ Calculated by taking the mean mortality probability and adding 0.5 standard deviations.

¶ All high and low prices are calculated by taking the average costs and multiplying to reflect the differences between the qualities.

following p and q values:

$$p = \frac{29}{1,890,000} = 0.000015$$

$$q = \frac{2500}{1,890,000} = 0.0013.$$

By substituting these values into Equation (4), the resulting K is

$$K = \frac{1.3 - 0.50}{\frac{1.54 \times 10^{-6}}{0.000015} + \frac{3.48 \times 10^{-8}}{0.0013}} \cong 8.$$

We also incorporated multiple habitat qualities into our application, by modifying Equations (A7) and (A8) to include two qualities in both breeding and wintering habitat (refer to Table A2 for parameter values used). We assumed that there is an equal amount of high- and low-quality habitat for both breeding and wintering habitats. Our simulations found that the optimal proportions of habitat purchased are

$$p_{\text{high_opt}} = 0.0001736 \cong 164 \text{ ha}$$

$$p_{\text{low_opt}} = 0 = 0 \text{ ha}$$

$$q_{\text{high_opt}} = 0.00001443 \cong 95.3 \text{ ha}$$

$$q_{\text{low_opt}} = 0 = 0 \text{ ha}.$$

The values of p_{opt} and q_{opt} are the averages of the two qualities purchased:

$$p_{\text{opt}} = \frac{0.0001755 + 0}{2} = 0.00008777$$

$$q_{\text{opt}} = \frac{0.0001009 + 0}{2} = 0.00005045.$$

Therefore, the resulting carrying capacity for this purchase equals:

$$K = \frac{1.65 - 0.45}{\frac{1.54 \times 10^{-6}}{0.00008681} + \frac{3.48 \times 10^{-8}}{0.00005045}} \cong 65.$$