



Essay

Nonbreeding-Season Drivers of Population Dynamics in Seasonal Migrants: Conservation Parallels Across Taxa

Facteurs hors reproduction intervenant sur la dynamique des populations de migrateurs saisonniers : analogie entre divers taxons

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ABSTRACT. For seasonal migrants, logistical constraints have often limited conservation efforts to improving survival and reproduction during the breeding season only. Yet, mounting empirical evidence suggests that events occurring throughout the migratory life cycle can critically alter the demography of many migrant species. Herein, we build upon recent syntheses of avian migration research to review the role of non-breeding seasons in determining the population dynamics and fitness of diverse migratory taxa, including salmonid fishes, marine mammals, ungulates, sea turtles, butterflies, and numerous bird groups. We discuss several similarities across these varied migrants: (i) non-breeding survivorship tends to be a strong driver of population growth; (ii) non-breeding events can affect fitness in subsequent seasons through seasonal interactions at individual- and population-levels; (iii) broad-scale climatic influences often alter non-breeding resources and migration timing, and may amplify population impacts through covariation among seasonal vital rates; and (iv) changes to both stationary and migratory non-breeding habitats can have important consequences for abundance and population trends. Finally, we draw on these patterns to recommend that future conservation research for seasonal migrants will benefit from: (1) more explicit recognition of the important parallels among taxonomically diverse migratory animals; (2) an expanded research perspective focused on quantification of all seasonal vital rates and their interactions; and (3) the development of detailed population projection models that account for complexity and uncertainty in migrant population dynamics.

RÉSUMÉ. À cause des contraintes logistiques, les seuls efforts de conservation des migrateurs saisonniers se limitent souvent à l'augmentation du taux de survie et du succès de reproduction durant la saison de reproduction. Pourtant, des indices de nature empirique de plus en plus nombreux semblent indiquer que les événements se produisant tout au long du cycle migratoire peuvent influencer grandement l'abondance de bon nombre d'espèces migratrices. Cet article présente une synthèse des recherches sur la migration aviaire afin de réviser le rôle des saisons hors reproduction dans la détermination de la dynamique des populations et du degré d'adaptation de différents taxons migrateurs, dont les Salmonidés, les mammifères marins, les Ongulés, les tortues marines, les papillons et de nombreux groupes d'oiseaux. Nous traitons de plusieurs similitudes entre ces divers migrateurs : (i) la survie hors reproduction a tendance à avoir une grande influence sur la croissance de la population; (ii) les événements hors reproduction peuvent influencer le degré d'adaptation au cours des saisons subséquentes en raison des interactions saisonnières à l'échelle de l'individu et de la population; (iii) les conditions climatiques à grande échelle affectent souvent les ressources hors nidification et la phénologie de la migration, et peuvent amplifier les impacts sur les populations à cause de la covariance des taux vitaux saisonniers; (iv) les changements relatifs aux milieux fréquentés, tant pendant la période de reproduction qu'en dehors de celle-ci, peuvent avoir des conséquences importantes sur l'abondance et la tendance des populations. Enfin, nous émettons les recommandations

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qui suivent car nous croyons que la recherche en conservation sur les migrateurs saisonniers en profitera : (1) reconnaître les analogies existant entre les animaux migrateurs de différents taxons; (2) orienter la recherche sur la quantification de tous les taux vitaux saisonniers et de leurs interactions; et (3) élaborer des modèles de projection de populations détaillés qui tiennent compte de la complexité et de l'incertitude inhérentes à la dynamique des populations migratoires.

Key Words: *carry-over; demography; migration; nonbreeding; seasonal interaction; survivorship*

INTRODUCTION

It is well understood that demographic fluctuations of populations living in seasonal environments are driven by events that occur throughout the year (Thompson 1959, Lack 1968, Fretwell 1972, Buehler and Piersma 2008). Variation in vital rates (growth, births, deaths) among seasons, and interactions between them may be particularly relevant to the population dynamics of "[seasonal migrants](#)" (Fig. 1), where individuals are exposed to multiple, and potentially divergent, environmental conditions in geographically separated habitats. Indeed, trade-offs between seasonal/geographic fitness costs and benefits led to the evolution of migratory behavior itself (Appendix 2). Although explicit recognition of seasonal effects is necessary for a complete assessment of the dynamics of any population, logistical constraints have often limited knowledge and conservation efforts for long-distance migrants to the breeding season only.

The importance of "[nonbreeding events](#)" to the conservation of migratory populations is becoming clearer as many face increasing rates of anthropogenically-induced environmental change. Current problems include disturbances to songbird wintering grounds (e.g., Robbins et al. 1989), depletion of critical stopover fuel sources for shorebirds (e.g., Baker et al. 2004), damming of rivers used by migrating fishes (e.g., Ratner et al. 1997), and disruption of ungulate migration routes (e.g., Bolger et al. 2008). Among migratory birds, conditions encountered in nonbreeding habitats have been linked to changes in abundance (Sherry et al. 2005), to reproduction (Norris et al. 2004a, Drent et al. 2006), and to persistence of declining populations (Robbins et al. 1989, Moore et al. 1995, Baker et al. 2004). Events outside of the breeding season may have been major contributors to population decline for migratory reptiles (Crowder et al. 1994), for fish (Wilson 2003), for ungulates

(Bolger et al. 2008), and for marine mammals (Kraus et al. 2005). Climatic changes (IPCC 2007) are also altering nonbreeding habitats, reducing migrants' physical preparedness for breeding (Friedland 1998, Bairlein and Huppopp 2004, Ward et al. 2005), and leaving their reproductive phenology out of synch with food availability (Stenseth and Myrsterud 2002, Drent et al. 2003, Both et al. 2006).

Migratory species belonging to very different taxonomic groups face parallel challenges in coping with change occurring in multiple habitats, and we argue that an increased awareness of these parallels will not only help to guide research efforts for particular taxa, but has the potential to help improve the effectiveness of conservation efforts. Here, we build upon recent syntheses of seasonal avian migration (e.g., Norris 2005, Dingle 2006, Newton 2006) to review (i) the role of nonbreeding survival in population dynamics of migrants, (ii) the impacts of nonbreeding events on subsequent reproduction and survival, and (iii) the consequences of these effects for population abundance and persistence, both generally and in relation to changing climatic conditions. Overall, we highlight the relevance of migratory bird research to studies of other migrants (see also Martin et al. 2007, Bolger et al. 2008, Robinson et al. 2008, Sherrill-Mix et al. 2008), and make specific recommendations for the incorporation of seasonal dynamics into conservation research and planning for migratory species.

DEMOGRAPHIC ROLE OF THE NONBREEDING SEASON

Ideally, the demographic importance of events during each season should be evaluated by incorporating the variation in vital rates throughout the life cycle into a model of population growth, and estimating the sensitivity of population dynamics to

Predation is the key mortality factor for migrating caribou and elk, for salmonids during their nonbreeding marine phase, and for sea turtle hatchlings during their first oceanic journey (Bergerud and Elliot 1986, Hansen and Quinn 1998, Hebblewhite and Merrill 2007, Harewood and Horrocks 2008). Weather conditions also influence survival, especially during migration (Newton 2007): storm events often result in high mortality for migrating birds (Butler 2000, Jones et al. 2004), and extreme fluctuations in temperature or precipitation reduce survival for both birds and fish (e.g., Möller 1989, Hansen and Quinn 1998). Deterioration of habitats used during the nonbreeding season has been implicated in declines of passerines, fish, and mammals, and climatic factors may indirectly affect survivorship by altering nonbreeding habitat or food availability (e.g., Fryxell 1987, Mduma et al. 1999, Sillett et al. 2000).

Quantitative comparisons of nonbreeding mortality across taxa are not yet possible, due to differences in estimation technique or time frame. For instance, studies reporting high migration mortality in passerines, salmonids, and ungulates (Sillett and Holmes 2002, Kareiva et al. 2000 and Hebblewhite and Merrill 2007) used different methods and time intervals than studies finding low rates of migration mortality in passerines and waterfowl (Ketterson and Nolan 1982, Gauthier et al. 2001). Moreover, many of the available estimates of nonbreeding survivorship represent “apparent” survival, i.e., the annual return rate of individuals to a monitored site. Given that the broad geographic areas covered by long-distance migrants may result in underestimation of dispersal, such approximations will greatly overestimate actual mortality unless they account for site fidelity or emigration (e.g., Friedland et al. 1993, Ruggerone et al. 2003, Jones et al. 2004, but see Cilimburg et al. 2002).

Reliable seasonal demographic estimates should increase with novel statistical and technological developments (Table 1). For example, long-term programs of physical marking of migrants and associated quantitative modeling permit better measurement of seasonal survivorship (e.g., Gauthier et al. 2001, Table 1), and studies based at nonbreeding areas are improving estimates of stationary nonbreeding (i.e., winter) mortality (e.g., Marra and Holmes 2001, Madsen et al. 2002, Sillett and Holmes 2002). New statistical tools also permit the analysis of incomplete data, as well as

the inclusion of information from one population in the modeling of another, by explicitly describing error and uncertainty terms (e.g., Bayesian integrated population models: Besbeas et al. 2002, Hoyle and Maunder 2004; or state-uncertainty mark-recapture models: Pradel 2005). Nonetheless, any permanent emigration of individuals from a study site would still bias survivorship estimates derived from these models, such that technological developments in the tracking of individuals across seasons may be required to further refine demographic estimates (e.g., satellite and radio tags; see Table 1).

Patterns of age-specific mortality during nonbreeding seasons are largely parallel across taxa, with juveniles typically experiencing high mortality during their first migratory journey. Between fledging and arrival at wintering grounds, young birds face elevated risks from predation (Anders et al. 1997), from unfavorable weather (van der Jeugd and Larsson 1998, Menu et al. 2005), from lack of experience orienting (Baldaccini and Bezzi 1989, Wiltschko and Wiltschko 2003), from competition (Woodrey 2000, Yong et al. 1998), or from harvest (Francis et al. 1992, Menu et al. 2002). Hatch-year birds may continue to experience poorer over-winter survival or reduced body condition prior to spring migration (Conroy et al. 1989, Perez-Tris and Telleria 2002). Juvenile salmonids experience similarly high mortality during their first migration and at sea prior to breeding (Friedland 1998, Greene and Beechie 2004, Quinn 2005), and young sea turtles (Crowder et al. 1994) and ungulates (Fryxell 1987, Fancy et al. 1994, Owen-Smith et al. 2005) also show lower survival than breeding adults. The extent to which potentially high natal dispersal biases these estimates is uncertain, as dispersal rates for all ages remain poorly quantified.

Taxonomic parallels in sex-biased seasonal survival are less obvious. Migratory behavior is often sex-specific in birds, including differences in stopover patterns (Yong et al. 1998), migration timing (Phillips et al. 2005, Kokko et al. 2006), and nonbreeding philopatry (Robertson and Cooke 1999), but the demographic consequences are largely unknown (Rankin and Kokko 2007). There is no consistent sex-bias in nonbreeding mortality, even among well-studied migrants (e.g., waterfowl: Raveling et al. 1992, Menu et al. 2002), but documented differences usually appear to favor males. For example, competition for winter habitat among warblers results in male-biased physical

Table 1. Current tools used for the study of nonbreeding parameters in diverse seasonal migrant taxa and some of their applications.

Method	Characteristic measured	Taxonomic group(s)	Studies
INTRINSIC MARKERS			
Mitochondrial DNA haplotypes	migratory connectivity	shorebirds	Lopes et al. 2006
Microsatellite markers	nonbreeding population structure	ungulates; salmonids	Courtois et al. 2003, Fraser and Bernatchez 2005
	nonbreeding social behaviour	salmonids	Fraser et al. 2005
Stable isotopes	nonbreeding habitat use	passerines	Norris et al. 2004a, Hobson 2005
Trace elements	nonbreeding distribution, migratory connectivity	marine fish	Campana et al. 1999
Hormone levels	nonbreeding habitat impacts	passerines	Marra and Holberton 1998
INDIVIDUAL TRACKING			
Geocator tags	migratory connectivity, migration speed	passerines	Stutchbury et al. 2009
Satellite tags	migratory connectivity, population structure	marine fish	Block et al. 2005
	nonbreeding distribution, critical habitat	sea turtles	James et al. 2005
	migration route, timing	waterfowl; sea turtles	Fox et al. 2003, Sherrill-Mix et al. 2008
Passive integrated transponder tags	inter-breeding intervals	sea turtles	Saba et al. 2007
Radio tags	post-fledging survivorship	passerines	Anders et al. 1997
	migration routes and timing	ungulates	Ferguson and Elkie 2004
Electronic data-log tags	nonbreeding distribution, migratory connectivity	marine fish; seabirds	Hunter et al. 2004, Phillips et al. 2005
Mark-recapture	seasonal nonbreeding survivorship	waterfowl; passerines	Gauthier et al. 2001, Sillett and Holmes 2002
Multi-state mark-recapture	migratory stopover behaviour	passerines	Schaub et al. 2004, Calvert et al. 2009

(con'd)

METHOD COMBINATIONS

Satellite tags, molecular markers	gene flow between migrants, residents	ungulates	Boulet et al. 2007
	migratory connectivity, population structure	passerines	Clegg et al. 2003
Stable isotopes, mark-recapture	migratory connectivity, nonbreeding habitat	shorebirds	Gunnarsson et al. 2005
Remote sensing, mark-recapture	nonbreeding distribution	passerines	Szep and Möller 2005

MODELING TOOLS

Population projection models	importance of nonbreeding survival	sea turtles; shorebirds	Caswell 2001, Crowder et al. 1994, Calvert et al. 2006
Geographic Information Systems	critical nonbreeding habitat location	passerines; butterflies	Villard and Maurer 1996, Oberhauser and Peterson 2003
	mapping of migration vs. shipping routes	marine mammals	Firestone et al. 2008
	predation risk to migrants vs. residents	ungulates	Hebblewhite and Merrill 2007
Habitat modeling	importance of stopover habitat	birds (general)	Tankersley and Orvis 2003
Evolutionary programming	habitat needs during migration	ungulates	Boone et al. 2006
Dynamic optimization modeling	effectiveness of conservation strategies	passerines	Martin et al. 2007
Integrated population models	nonbreeding links to population growth	birds; marine mammals	Besbeas et al. 2002, Hoyle and Maunder 2004
Dynamic state modeling	effects of seasonal habitat change	waterfowl	Pettifor et al. 2000

condition, apparent survival, and sex ratio (Holmes et al. 1989, Sherry and Holmes 1996, Marra and Holberton 1998, Marra and Holmes 2001). Higher nonbreeding mortality among females is also apparent in some salmonids (Holtby and Healey 1990, Spidle et al. 1998) and whales (Fujiwara and Caswell 2001).

Sensitivity of nonbreeding vital rates

The "[sensitivity](#)" or "[elasticity](#)" (hereafter just "sensitivity") of vital rates is a measure of the contribution of each parameter to population

growth, relative to all other rates over the life cycle. Theory predicts that long-lived "survival" species will be more sensitive to nonbreeding events, whereas short-lived "reproductive" species are more sensitive to breeding parameters (Saether et al. 1996, Heppell et al. 2000). Broad-scale comparisons indicate that population growth across a wide diversity of migrants is almost always more sensitive to adult survival, often a surrogate for nonbreeding survival, than to reproductive parameters (Pfister 1998, Saether and Bakke 2000). Indeed, high sensitivity of adult/nonbreeding survival has been demonstrated for seabirds

(Cuthbert et al. 2001, Ezard et al. 2006), shorebirds (Hitchcock and Gratto-Trevor 1997, Calvert et al. 2006), waterfowl (Hoekman et al. 2006), songbirds (Fletcher et al. 2006), marine mammals (Brault and Caswell 1993, Caswell et al. 1999, Runge et al. 2004), ungulates (Fancy et al. 1994, Mduma et al. 1999), and salmonids (Greene and Beechie 2004). While breeding-season effects such as food limitation or predation likely also play an important role in population regulation, particularly for the shorter-lived species (Saether et al. 1996, Heppell et al. 2000), threats to survival outside the breeding season thus appear to have strongly impacted the populations dynamics of migrants studied to date.

Cross-seasonal nonbreeding effects

Individual-level seasonal interactions

Whereas vital rates are estimated at the scale of the population, migration is accomplished by individual animals, and the experiences of an individual in one season thus inevitably affect its subsequent fitness (Dingle 1996, Newton 2004, Norris 2005). Although in the long-term there must theoretically be trade-offs between different vital rates (see McNamara and Houston 2008 and references therein), these individual-level seasonal interactions, sometimes termed “carry-over effects”, generate short-term positive correlations among consecutive vital rates (Figs. 2,3) and have become the focus of several studies on the fitness consequences of nonbreeding events in migratory birds (Norris 2005, Runge and Marra 2005). Specifically, differential winter habitat use was shown to alter the physiological condition of passerines prior to spring migration (Marra and Holberton 1998, Bearhop et al. 2004), an effect which can subsequently influence migration phenology (Saino et al. 2004), reproductive success (Norris et al. 2004a), and survival (Marra and Holmes 2001). Similarly, individual experiences during migratory travel or stopover may further influence subsequent fitness (Fig. 2, Table 2). Pre-breeding resources are particularly essential to female reproductive success and survival of shorebirds and waterfowl (Alisauskas 2002, Drent et al. 2006, Kéry et al. 2006).

Individual-level seasonal interactions are not unique to migratory birds (Table 2). Survival and reproduction of salmonids, for instance, are strongly influenced by previous climate- and

competition-driven variation in ocean-phase growth (Ruggerone et al. 2003, Beamish et al. 2004, Friedland et al. 2005). Migratory ungulates probably also experience seasonal interactions in a manner parallel to that seen in birds, yet these remain little studied (Bolger et al. 2008). Given that individual correlations can persist for multiple seasons or even years (Pienkowski and Evans 1984, Marra and Holmes 2001), they merit incorporation into assessments of migratory population dynamics, particularly in taxa other than avian migrants (Doak et al. 2005, Runge and Marra 2005).

Population-level seasonal interactions

Seasonal interactions also operate at the level of the migratory population (Runge and Marra 2005, Figs. 2,3, Table 2). Since Fretwell’s (1972) proposal that population size in the breeding season is driven by habitat availability in other seasons, growing evidence suggests that density-dependent factors during one season affect fitness parameters in later life stages for migratory birds (Ketterson and Nolan 1982, Dit Durell et al. 1997, Newton 2004, 2006). Density-dependent regulation across seasons, such as reduced fecundity with high breeder density (i. e., reflecting elevated prior survival or productivity; Sillert and Holmes 2005, Gunnarsson et al. 2006), could produce negative correlations between consecutive demographic traits for any seasonal migrant. A negative relationship between reproductive success and nonbreeding survivorship driven by limiting seasonal resources could then buffer overall abundance changes (Fig. 3). Regulation of avian migrant populations based on nonbreeding resources has been hypothesized a number of times (Robbins et al. 1989, Rappole and McDonald 1994, Buehler and Piersma 2008), but stronger empirical evidence is still needed to confirm impacts on survival and abundance (Latta and Baltz 1997, Sherry et al. 2005). Some nonavian migrants have also shown evidence of nonbreeding density dependence, but much empirical work is still needed (e.g., mammals: Bolger et al. 2008; salmonids: Greene and Beechie 2004, Quinn 2005).

The population dynamics of seasonal migrants depend upon the connections between breeding and nonbreeding populations (Esler 2000), and the strength of nonbreeding population regulation may vary with a population’s “[migratory connectivity](#)” (Webster et al. 2002). The degree to which individuals from the same breeding area overlap in their nonbreeding distribution, and vice versa, is

Fig. 2. Generalized schematic illustrating the influences of seasonal events on the population dynamics of seasonal migrants. Arrows represent direct seasonal fitness impacts (solid black arrows), cross-seasonal interactions (dashed grey arrows), covariation in seasonal environments (solid grey arrows), and sensitivities of population growth to seasonal vital rates (dotted black arrows). Note that terminology applies generally to avian migrants, but concepts extend to all seasonal migrants (e.g., “winter” refers to any primarily stationary nonbreeding season). See Table 2 for definitions and literature examples of each seasonal influence and their links to population growth.

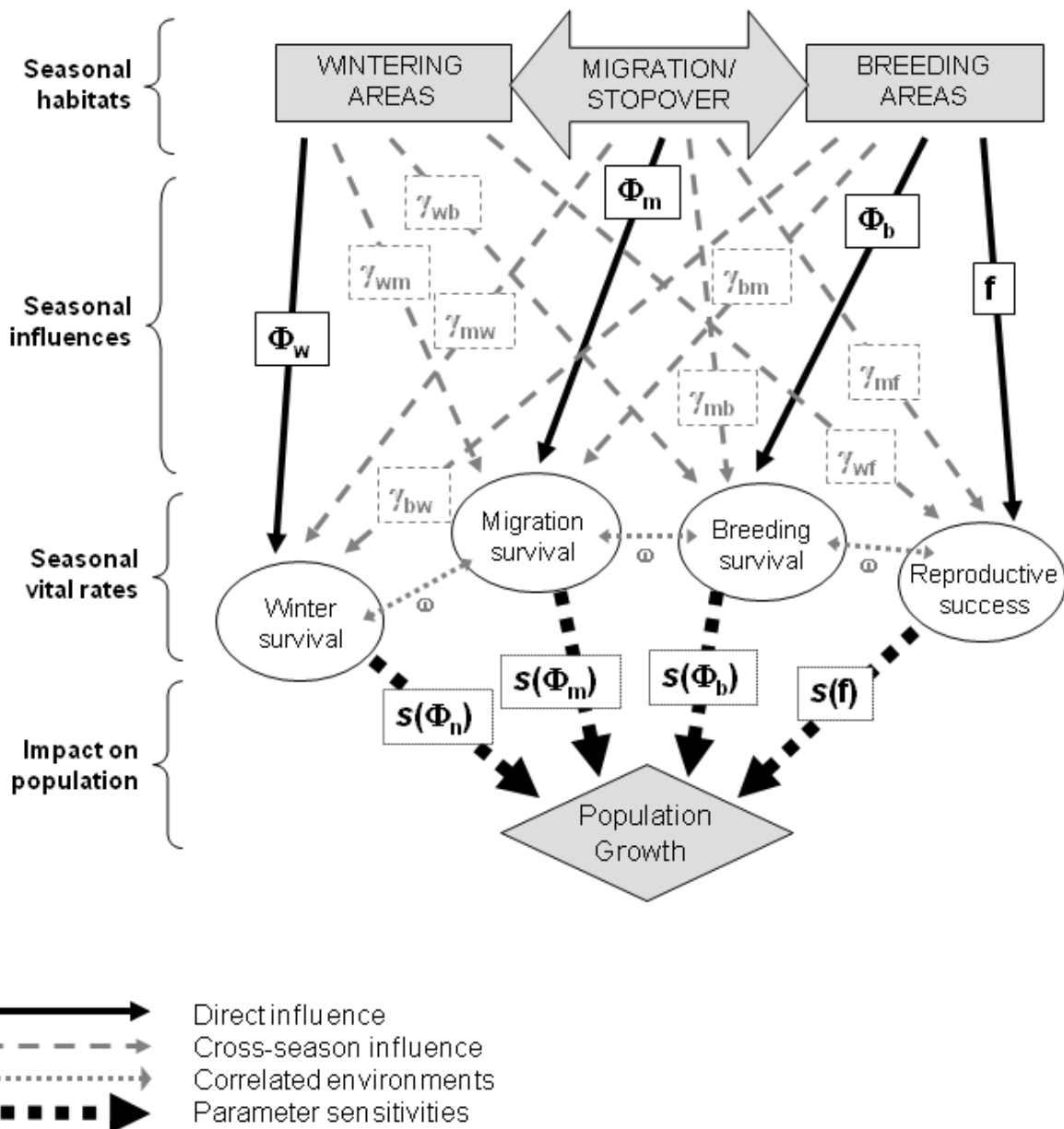


Fig. 3. Three levels of cross-seasonal nonbreeding influences upon population dynamics of seasonal migrants, illustrating the required nonbreeding characteristic, the subsequent season impact, and the consequences for population growth; linear relationships are assumed for simplicity, and each level is presented independently from others (i.e., without accounting for potential interactions among levels). At the individual level, carry-over of individual condition or migration timing from one season to another can result in short-term positive correlations among seasonal vital rates and between nonbreeding vital rates and population growth. At the population level, density-dependence in one season can cause negative relationships between seasonal vital rates which may buffer overall effects on population growth. At the environmental level, broad-scale climatic trends can cause positive covariation among seasonal environments and thus among consecutive seasonal vital rates, with the potential for magnified climatic impacts on population growth. See Table 2 and text for further details and literature examples.

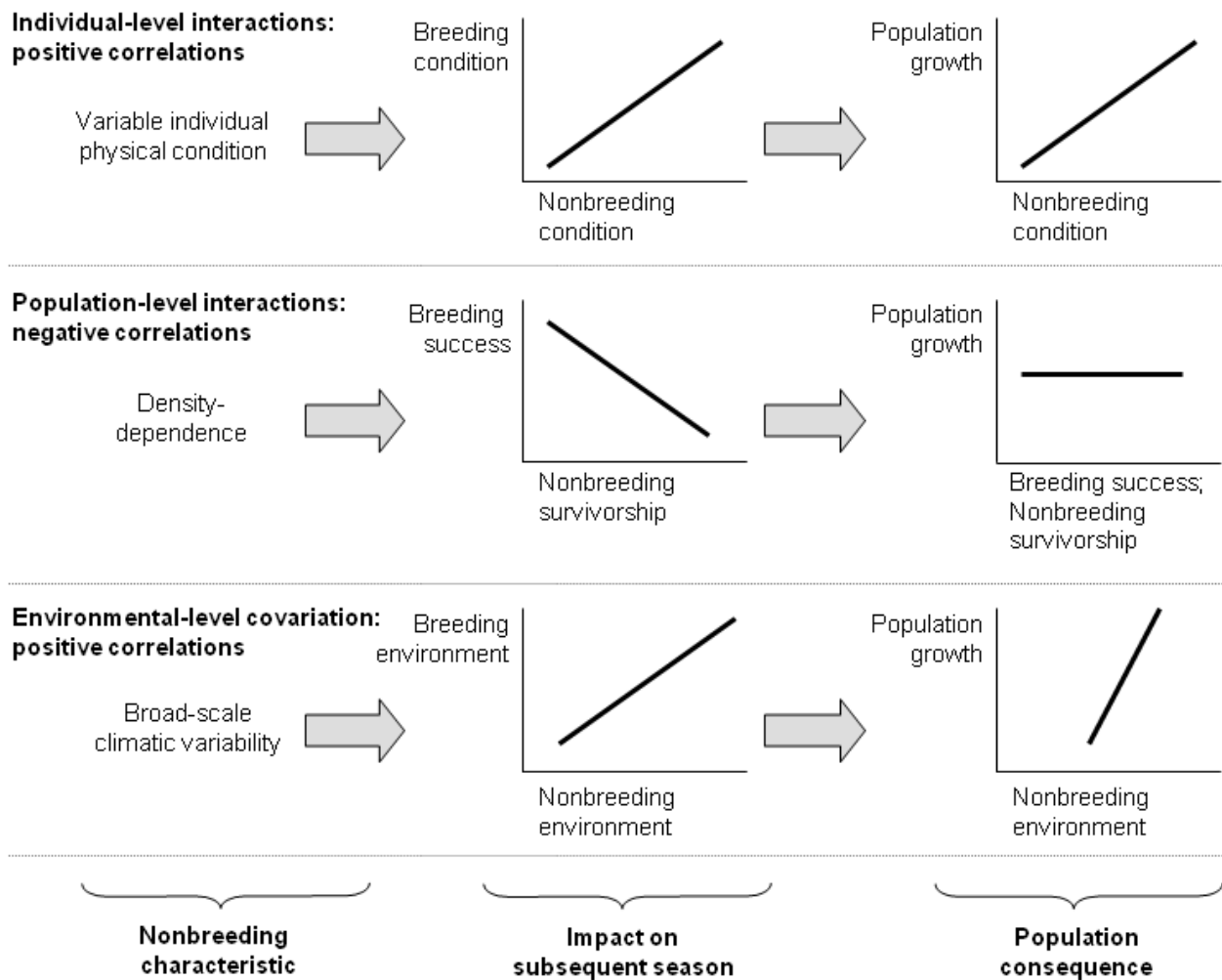


Table 2. Conceptual links between seasonal habitats and population growth for seasonal migrants, as shown in Figure 2, with a description of each link and the level of cross-season interactions (see Figure 3). Note that “winter” refers to any primarily-stationary nonbreeding season.

Symbol	Parameter		Description	Examples
DIRECT FITNESS INFLUENCE				
Φ_w	Winter survivorship	magnitude	age-dependent; influenced by predation, habitat quality	Conroy et al. 1989, Conway et al. 1995, Marra & Holmes 2001
		variance	varies with environmental conditions	Mduma et al. 1999, Grosbois & Thompson 2005, Schaub et al. 2005, Kéry et al. 2006
Φ_m	Migration survivorship	magnitude	age-dependent; influenced by habitat, energetic constraints	Gauthier et al. 2001, Sillett and Holmes 2002, Menu et al. 2005
		variance	varies with environmental conditions	Friedland et al. 1993, Butler 2000, Cuthbert et al. 2001
Φ_b	Breeding survivorship			
f	Reproductive success			
CROSS-SEASON FITNESS INFLUENCE				
		Level		
γ_{wm}	Winter effect on migration survivorship	individual, population	winter habitat competition affects survival during migration via individual body condition	Marra and Holmes 2001, Sillett & Holmes 2002
γ_{wb}	Winter effect on breeding survivorship	individual, population	availability of winter resources affects later survival via individual body condition, density dependence	Sherry & Holmes 1996, Beamish et al. 2004, Friedland et al. 2005
γ_{wf}	Winter effect on breeding success	individual, population	availability of winter resources affects reproduction via individual condition, migration timing, density-dependence	Norris et al. 2004a, Newton 2004, Saino et al. 2004, Moore et al. 2005
γ_{mw}	Migration effect on winter survivorship	population	climate-driven variation in resources at fall staging site influence overall (presumably winter) survival	Schaub et al. 2005
γ_{mb}	Migration effect on breeding survivorship	individual	availability of migration/stopover resources affects subsequent survival via individual body condition	Schmutz & Ely 1999, Baker et al. 2004, Kéry et al. 2006, Newton 2006
γ_{mf}	Migration effect on breeding success	individual	availability of migration/stopover resources affects reproduction via individual condition, migration timing	Alisauskas 2002, Mainguy et al. 2002, Drent et al. 2003, 2006, Reed et al. 2004

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γ_{bw}	Breeding effect on winter survivorship	individual	juveniles from favourable breeding habitats are more likely to obtain access to good winter habitat	Dit Durell et al. 1997, Gunnarsson et al. 2005
γ_{bm}	Breeding effect on migration survivorship	individual	juveniles departing breeding grounds in poor weather, poor condition or late have lower migration survival	Menu et al. 2005

CLIMATIC INFLUENCES

ω	Environmental covariation		broad-scale climatic variation across seasons results in covariation among consecutive seasonal vital rates	Sillett et al. 2000, Grosbois & Thompson 2005, Stenseth & Mysterud 2005, Lee et al. 2007
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SENSITIVITIES

$s()$	Sensitivity of population growth to seasonal vital rates		population growth sensitivity to annual adult survival usually high; seasonal sensitivities poorly known	Caswell et al. 1999, Greene & Beechie 2004, Calvert et al. 2006, Fletcher et al. 2006
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likely to influence the relative importance of breeding and nonbreeding habitats on demographic fluctuations (Webster et al. 2002, Webster and Marra 2005). Interactions between breeding and nonbreeding events are likely to be amplified in populations with strong migratory connectivity, and thus its inclusion in population models will permit more effective evaluation of alternative conservation strategies (e.g., Martin et al. 2007). Migratory connectivity has now been studied in numerous avian migrants through the use of new tools such as genetic markers and stable isotopes (e.g., Clegg et al. 2003, Lopes et al. 2006, Table 1). Similarly, tracking of individual fish has allowed divergent breeding populations to be distinguished during nonbreeding seasons (e.g., Campana et al. 1999, Hunter et al. 2004, Fraser and Bernatchez 2005), and the identification of seasonal population structuring is now gaining attention in other taxa (e.g., caribou: Boulet et al. 2007).

Climatic impacts and correlations

Migrants are exposed to environmental variation in several geographic areas, such that current climatic changes may magnify any nonbreeding season influences on population dynamics. Projected increases in the frequency of extreme weather (IPCC 2007) might increase direct mortality during

migratory travel (Butler 2000, Newton 2007), and could further affect subsequent survival and/or reproduction via individual- or population-level seasonal interactions. Nonbreeding survival of migrants fluctuates strongly in response to environmental conditions (Friedland et al. 1993, Frederiksen et al. 2005), and the omission of true (process) variance from population analyses could lead to inaccurate estimates of growth rate or population viability (Beissinger and Westphal 1998, Caswell 2001) and misleading assessments of the status of migratory species (Hitchcock and Gratto-Trevor 1997, Gaillard et al. 2000, Cuthbert et al. 2001). Future climatic change may increase variability in migrants' nonbreeding survival and thus alter population trajectories (Friedland et al. 2005, Grosbois and Thompson 2005, Laaksonen et al. 2006), as the ability of migrants to adapt to climatic changes remains uncertain (Lemoine and Bohning-Gaese 2003, Bêty et al. 2004, Both et al. 2005, Appendix 2).

Climatic effects also have the potential to elicit rapid population change through positively correlated vital rates (Lee et al. 2007, Fig. 3), as broad-scale climatic variation can affect local weather, and hence seasonal vital rates, across several consecutive seasons (Sillett et al. 2000, Stenseth and Mysterud 2005). Indeed, there is evidence of covariation in vital rates both within and among

populations (Schaub et al. 2005, Ezard et al. 2006), with implications for parameter sensitivities and population trajectory (Doak et al. 2005, Adahl et al. 2006). Together with individual- and population-level seasonal interactions, "[environmental-level covariation](#)" among vital rates may thus drive complex relationships between nonbreeding seasons and population dynamics (Holmes 2007, Figs. 2,3, Table 2).

Recent climatic shifts have produced parallel responses among migratory taxa during the nonbreeding season (Robinson et al. 2008). Changes in the temperature/precipitation regime of nonbreeding sites are leading to altered timing of migration and breeding (Cotton 2003, Sims et al. 2004, Gunnarsson et al. 2006), and to changes in reproductive rates for many migrant species (e.g., Stenseth and Mysterud 2002, Weishampel et al. 2004, Lehikoinen et al. 2006, Table 3). The reproductive success of migratory birds breeding in both Europe and North America is also being shaped by climate-driven fluctuations in nonbreeding food availability (Saino et al. 2004, Ward et al. 2005, Laaksonen et al. 2006), while reproductive output in sea turtles fluctuates with broad-scale ocean cycles (Saba et al. 2007). Continued shifts in climate could further alter migration routes or geographic distribution (Sutherland 1998, Austin and Rehfish 2005, Gauthreaux et al. 2005), and ultimately the capacity of nonbreeding habitats to sustain migratory populations (e.g., Oberhauser and Peterson 2003). The susceptibility of all seasonal migrants to major global climatic shifts (IPCC 2007) is thus further justification for cross-taxa conservation planning.

DISCUSSION

Nonbreeding season relevance to population persistence

The above sections confirm the relevance of nonbreeding events to seasonal vital rates, but growing evidence also supports longer-term consequences for the abundance and persistence of threatened migrant populations (Table 3, see also review by Robinson et al. 2008). En-route habitats are critical to maintaining positive population growth in landbirds (Hutto 2000, Mehlman et al. 2005, Table 3), and habitat change in the tropics may have contributed to the reduced breeding

abundance of many species (Robbins et al. 1989, Rappole and McDonald 1994). The persistence of endangered whales and other migratory marine mammals is jeopardized by commercial shipping traffic (Runge et al. 2004, Kraus et al. 2005, Firestone et al. 2008), while fisheries bycatch during migration and ocean-foraging threatens declining seabirds (Phillips et al. 2005). Commercial harvesting of fish during nonbreeding seasons could precipitate declines if the migratory connectivity to breeding populations is unknown (Campana et al. 1999, Beacham et al. 2005). Finally, shorebirds that exploit specific habitats for intense refuelling periods are particularly sensitive, as seen with the sudden decline of the Red Knot (*Calidris canutus*) attributed to changing food availability at a critical spring stopover site (Baker et al. 2004, Skagan 2006).

The importance of nonbreeding season vital rates to population dynamics is not unique to migratory animals, and in fact many of the seasonal influences discussed above apply equally to the conservation of nonmigrant animals and plants, e.g., nonmigratory amphibians or insects that use different habitats as juveniles and adults. But seasonal migrants are unique in the geographic scale of these differences, leaving them vulnerable to changes in several distant habitats as well to factors that might interrupt migratory travel. Globally, large-scale ungulate migrations are increasingly cut off by agricultural development and other anthropogenic habitat change (Berger 2004, Bolger et al. 2008), and entanglement of sea turtles in fisheries gear impedes breeding-based conservation efforts (Crowder et al. 1994, James et al. 2005). Reduced juvenile-to-spawner survival of salmon in estuarine and marine areas (Wilson 2003) has been linked to changing ocean climate conditions (Friedland et al. 1993, Hansen and Quinn 1998), while birds around the world are experiencing changes to critical pre-breeding migration resources (Norris et al. 2004b, Drent et al. 2006). Human and climatic impacts on natural systems are of immediate concern to all seasonal migrants, where the success or failure of conservation actions may hinge upon identification of seasonal drivers of population change. As noted by Bolger et al. (2008) regarding knowledge gaps in the population dynamics of migratory ungulates, insight borrowed from other migratory taxa, well-studied birds in particular, may therefore be key to developing appropriate research plans and effective conservation strategies.

Table 3. Examples of human-induced nonbreeding impacts on population dynamics of diverse seasonal migrants, as suggested by empirical studies.

Nonbreeding season event	Suggested population impact	Taxonomic group(s)	Studies
HABITAT CHANGE			
Tropical deforestation (winter habitat)	decline in abundance	passerines	Robbins et al. 1989, Rappole & McDonald 1994, Haney et al. 1998
	minor relative to other factors	passerines	Bohning-Gaese et al. 1993, Latta & Baltz 1997
Coastal habitat destruction	decline in abundance	shorebirds	Norris et al. 2004b, Drent et al. 2006
Depletion of stopover food source	reduced survival, abundance	shorebirds	Baker et al. 2004
Loss of winter, staging habitat	decline in abundance	waterfowl	Pettifor et al. 2000
Increase in agricultural development	increased migration survival	waterfowl	Gauthier et al. 2005
River damming (breeding/migration habitat)	reduced migration survival	salmonids	Ratner et al. 1997, Kareiva et al. 2000, Wilson 2003
	disruption of metapopulation	salmonids	Fraser et al. 2007
Agricultural development and fencing	decline in abundance	ungulates	Bolger et al. 2008
Human settlement, farming, fencing	interruption of migration route	terrestrial mammals	Berger 2004, Thirgood et al. 2004
CLIMATIC VARIABILITY			
Change in winter climate	fluctuations in abundance	butterflies	Vandenbosch 2003
Increase in winter/spring temperature	improved survival, reproduction	waterfowl	Lehikoinen et al. 2006, Kéry et al. 2006
Sudden weather changes, storms	mortality during migration	birds (various)	Newton 2007 (review)
Change in ocean temperature	reduced nonbreeding survival	salmonids	Friedland et al. 1993, Bisbal & McConnaha 1998
	variation in breeding frequency	seabirds, sea turtles	Lee et al. 2007, Saba et al. 2007
Variation in dry-season rainfall	reduced annual survival	ungulates	Owen-Smith et al. 2005

(con'd)

Decline in climate-linked food sources	reduced reproductive success	birds (general)	Bairlein & Huppopp 2004, Ward et al. 2005, Lee et al. 2007
Variable seasonal rates of change	mismatched breeding phenology	shorebirds; passerines	Stenseth & Mysterud 2002, Drent et al. 2003, Both et al. 2006
MORTALITY/DISTURBANCE			
Sport harvest	reduced nonbreeding survival	waterfowl; salmonids	Menu et al. 2002, Calvert & Gauthier 2005, Quinn 2005
Declining sport harvest	increased survival	waterfowl	Gauthier et al. 2005
Disturbance at staging sites	reduced pre-breeding condition	waterfowl	Mainguy et al. 2002, Klaassen et al. 2006
Ship collision/gear entanglement	reduced nonbreeding survival	marine mammals	Caswell et al. 1999, Runge et al. 2004, Kraus et al. 2005
Fisheries bycatch	reduced nonbreeding survival	marine reptiles; seabirds	Crowder et al. 1994, Cuthbert et al. 2001, James et al. 2005, Phillips et al. 2005

Recommendations

The use of many dispersed habitats by long distance migrants presents logistical constraints to the comprehensive estimation of seasonal vital rates. Migrants are typically stationary when breeding, allowing for relatively accurate estimates of breeding parameters, whereas in nonbreeding seasons they travel vast distances across harsh or inaccessible environments (Alerstam et al. 2003). Many seasonal migrants, especially birds, also breed in high-latitude areas, corresponding with generally greater economic prosperity and better research funding. Nonbreeding-based conservation is often further limited by management jurisdictions. Canada's Species at Risk Act, for example, prohibits destruction of listed species' "critical habitat", but only within Canadian boundaries, whereas in other regions the geographical range of migrants extends well beyond the limits of protected areas (e.g., Thirgood et al. 2004). Nonetheless, with modern tools permitting individual tracking and temporal hindsight into the life cycles of diverse migrant taxa (Table 1), the necessary shift in conservation ideology toward a comprehensive cross-seasonal perspective can be realized via three principal actions:

Conservation plans must move away from the breeding-centric. Nonbreeding season parameters are not the only drivers of demography, and thus it is clearly important to continue efforts to maintain or increase survivorship and reproduction of migrants during the breeding season in situations where population regulation depends largely on events during reproduction. However, more explicit recognition of the connections between seasons is required to guide allocation of resources effectively (Martin et al. 2007). Habitat alteration, climatic change, and direct mortality during nonbreeding seasons have important consequences for diverse migratory taxa (Table 3). In salmonid fishes, recovery efforts must extend beyond spawning streams (e.g., Kareiva et al. 2000, Wilson 2003) to address ocean-phase mortality and near-shore habitats (Bisbal and McConnaha 1998, Greene and Beechie 2004). Protection of stopover areas, including a better understanding of the scales at which these sites should be viewed (Buler et al. 2007), should be integral to songbird conservation (Moore et al. 1995, Hutto 2000), and monitoring of songbird winter habitat may reveal the causes of some population declines (Dit Durell et al. 1997, Holmes 2007). A cross-seasonal perspective is most urgently required for endangered populations, where identification of nonbreeding habitat is critical to recovery, e.g., for leatherback sea turtle

Dermochelys coriacea (James et al. 2005, Sherrill-Mix et al. 2008), and where damage to these habitats may be ignored under breeding-focused conservation efforts, e.g., for Kirtland's Warbler *Dendroica kirtlandii* (Haney et al. 1998). When nonbreeding information is still lacking, knowledge gained from studies of other migrants may provide valuable insight into demographic patterns or conservation needs common to diverse migratory taxa (see Martin et al. 2007, Bolger et al. 2008, Robinson et al. 2008, Sherrill-Mix et al. 2008).

Season-specific vital rates, their relative contributions to population growth, and the within-population variation in these parameters must be better quantified. The impact of threats to nonbreeding survival relative to factors influencing survival and breeding success on the breeding grounds must be measured before we can identify the most critical habitats or most vulnerable age classes (e.g., Crowder et al. 1994, Mduma et al. 1999, Owen-Smith et al. 2005). Current sensitivity estimates support the key role of nonbreeding vital rates in the population dynamics of most migratory species, but improved quantification of survival, dispersal and reproductive parameters and their sensitivities will enable conservation biologists to anticipate nonbreeding events that threaten the persistence of species already at risk (e.g., Baker et al. 2004). When possible, estimates of vital rates should also be sex-specific, as projections of population dynamics may be highly dependent upon recognition of sex differences in survival and reproduction (Ezard et al. 2006, Rankin and Kokko 2007).

Conservation of migrants must include the development of population growth models that incorporate seasonal components of migratory life cycles. A partitioning of mortality risks and reproductive influences among all seasonal habitats, as well as an improved understanding of how those seasonal parameters interact, will allow conservation goals and management actions to be specifically tailored to particular seasons or life stages (e.g., Baker et al. 2004, Calvert and Gauthier 2005). Through assessment of both sensitivity and variability in vital rates, projection models will permit the identification of the optimal targets for conservation, and taxonomic parallels mean that model development for poorly-known taxa can build upon demographic characteristics of other migrants (Martin et al. 2007, Bolger et al. 2008).

Manipulation of highly-sensitive parameters might not always represent the best investment of resources (Mills et al. 1999, Hoekman et al. 2006): if nonbreeding survival is near the maximal rate possible or otherwise invariable, efforts aimed at increasing survival during this period might yield only minor changes to population growth and more flexible vital rates will be better conservation targets (Gaillard et al. 2000, Wemmer et al. 2001). Where seasonal data are sparse, population models could incorporate incomplete data or information from other similar migrants using methods that account for error and uncertainty (e.g., Besbeas et al. 2002, Hoyle and Maunder 2004). The inclusion of partial data, vital rate approximations, or data from other populations into projection models may fill critical gaps remaining in our understanding of seasonal migrants' complex population dynamics.

CONCLUSION

Some recent studies have effectively quantified nonbreeding influences in passerines (e.g., Runge and Marra 2005, Webster and Marra 2005). Others have established their significance across broader avian taxa (Newton 2004, 2006). Nevertheless, the heuristic value of this work to seasonal migrants as a whole, where nonbreeding effects demonstrated in birds may be equally critical to the dynamics of other migratory populations, has not yet been fully exploited (Bolger et al. 2008, Robinson et al. 2008). Our review highlights the need for a shift in migration research away from a single-season focus and toward explicit recognition of the complexity of migratory demography. At a minimum, this requires a multi-taxa and multi-seasonal perspective that encompasses the entire life cycle, including clearer recognition of how seasonal vital rates contribute to population growth and how they interact across temporal and spatial scales. Such an approach will require a more focused and standardized quantification of seasonal vital rates, and further development of population models that account for these interactions: attention to these details will enable a more preventative approach to conservation planning that projects future impacts of climatic and anthropogenic change. Only with such insight can we decipher the links between environment and demography necessary to the conservation of migratory populations.

Responses to this article can be read online at:
<http://www.ace-eco.org/vol4/iss2/art5/responses/>

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APPENDIX 1. GLOSSARY OF TERMS. Key words used in this review and their meanings in the current context; references cited refer to literature from which the terms derived or were discussed, but definitions may not be identical.

Carry-over (i.e., individual-level seasonal interactions) – influence of events occurring in one season on individual survival or reproduction in a subsequent season (Norris 2005)

Density-dependence (i.e., population-level seasonal interactions) – population regulation based on limited resources, taking the form of negative relationships between seasonal abundance (or its drivers) and subsequent fitness; e.g., a linear negative relationship between breeding success and nonbreeding survival (Sillett and Holmes 2005, Webster and Marra 2005)

Environmental-level covariation – climate-driven covariation between consecutive seasonal vital rates

Migratory connectivity – links between breeding and nonbreeding populations, i.e., the degree to which individuals from the same breeding area share nonbreeding areas and vice versa (Webster et al. 2002)

Nonbreeding events – changes occurring during stationary or migratory nonbreeding seasons that could have implications for the fitness of seasonal migrants, e.g., habitat alteration, direct mortality threats, reduction in resource availability, interruption of migration route

Seasonal interactions – effects of events or changes in one season on survival or reproduction in another season; can occur at individual-level, “carry-over”, or population-level, “density dependence” (Runge and Marra 2005)

Seasonal migrants – animals that make extended seasonal movements between geographically separated regions within their life cycle (e.g., Fig. 1); simply termed “migrants” in this review

Sensitivity or elasticity (of a vital rate) – absolute or proportional change in population growth rate λ resulting from a change in that parameter (Caswell 2001)

APPENDIX 2. NONBREEDING SEASONS AND THE EVOLUTION OF MIGRATION

Seasonal migration has evolved many times within diverse taxa (e.g., Pascual et al. 2001, Alerstam et al. 2003) and is expressed through a wide range of movement behaviours (Quinn and Myers 2004, Dingle 2006, Bolger et al. 2008). Migration will be favoured where the benefit gained from moving between habitats outweighs the fitness risks and energetic costs of the journey; seasonal and spatial variations in environmental conditions are therefore primary forces in its evolution (Fretwell 1972, Alerstam and Enckell 1979). Some theory suggests that migratory behaviour evolved primarily in response to the advantages of breeding in regions of seasonally high resource availability and safety for juveniles (Corkeron and Connor 1999, Friedland et al. 2005), especially where resources in the nonbreeding area were limited (Fretwell 1972, Cox 1968, 1985). Indeed, there is evidence today for competition during the nonbreeding season among many seasonal migrants (e.g., Pienkowski and Evans 1984, Perez-Tris and Telleria 2002, Ruggerone et al. 2003). Alternatively, the principal selection pressure might have been the survival advantage gained by individuals that migrated to less harsh, safer or more resource-rich environments after breeding (Lack 1968, Ketterson and Nolan 1982, Hebblewhite and Merrill 2007). Both scenarios involve the balancing of benefits and costs, in terms of energy acquisition and mortality risks, between breeding and nonbreeding seasons.

There is evidence that migratory behaviour continues to evolve in response to environmental changes or variation in nonbreeding habitats (Berthold et al. 1992). For instance, selection favours individual birds whose spring migration synchronizes breeding with peak resource availability (Kokko 1999, Drent et al. 2003, Bêty et al. 2004); heritability of migratory traits could thus allow migrants to adapt to changing climatic conditions experienced prior to breeding (Berthold and Pulido 1994, Both et al. 2005). Natural selection has also favored local adaptation to nonbreeding areas in migrating fish (e.g., Fraser and Bernatchez 2005), which could ultimately lead to speciation if it favored reproductive isolation between populations (Wood and Foote 1996). Nevertheless, the ability of migrants to adapt to rapid environmental changes may be also shaped by seasonal features such as migration distance, severity of nonbreeding habitat loss, correlations between seasonal environmental changes, or the strength of cross-seasonal migratory connectivity (Dolman and Sutherland 1994, Sutherland 1998, Webster et al. 2002, Lemoine and Bohning-Gaese 2003, Both et al. 2005).

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