Cross-scale environmental influences on migratory stopover behaviour

A N N A   M .   C A L V E R T *†,   P H I L I P   D .   T A Y L O R †   and   S A N D R A   W A L D E *
*Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1, †Atlantic Cooperative Wildlife Ecology Research Network, Biology Department, Acadia University, Wolfville, NS, Canada B4P 2R6

Abstract

Migratory species may be especially sensitive to climate change because their lifecycles are affected by dynamic ecological processes operating at global spatial scales. Insight into environmental effects upon *en route* decisions by migrants can therefore be a critical first step toward assessing their vulnerability to future climatic shifts. We extracted behaviour-related parameters from a recent formulation of multistate mark–recapture models, and used them to evaluate the importance of variation in local weather and broad-scale climate to decisions made by autumn passerine migrants at a coastal stopover site in Atlantic Canada. We found dramatic interannual fluctuations in the proportion of migrants that were transient (departing within a day of arrival), with annual average values ranging from 24% to 96% over the years 1996–2007. However, the relationships of stopover behaviour (transience and departure probability) to local weather (wind and precipitation) and to regional climatic fluctuations were similar across three distinct species groups and for birds of different fuel-loads, indicating the potential for both immediate (day-to-day) and long-term environmental influences (spanning several seasons). This cross-scale approach contributes valuable information toward the conservation of migrants in the face of a changing climate by (i) quantifying environmental influences on stopover behaviour in broad temporal and geographic contexts, and (ii) demonstrating largely parallel interannual variation in stopover site-use among birds with contrasting migratory timing and strategies.

Keywords: autumn, climate, departure, ENSO, mark–recapture, migration, NAO, passerine, stopover, weather

Received 5 November 2007; revised version received 1 July 2008 and accepted 16 July 2008

Introduction

Fluctuations in weather and resources likely shaped the evolution of migratory behaviour of many taxa, and environmental variability continues to influence the timing of current migratory journeys (Cohen, 1967; Gauthreaux, 1980; Wiener & Tuljapurkar, 1994; Alerstam et al., 2003; Macmynowski et al., 2007). Migrants must respond to ongoing changes in their environment because of the high energetic demands of sustained long-distance travel (Klaassen & Lindström, 1996; McWilliams et al., 2004) and the negative fitness consequences of delays or diversions (Møller, 1994; Drent et al., 2003). Furthermore, there is increasing evidence that variation in weather during nonbreeding seasons affects the subsequent physical condition, reproduction and survival of migrants (Marra et al., 1998; Bearhop et al., 2004; Norris et al., 2004; Lehikoinen et al., 2006; Sedinger et al., 2006). The occurrence of such far-reaching weather-related fitness effects across seasons and geographical locations suggests that climatic influences continue to exert important selective pressures on migrants.

Migratory animals face particular risks from a changing climate. Their dependence on geographically separated habitats leaves them susceptible to potentially divergent climatic influences during different portions of their life cycle at both local and regional scales (Gauthreaux, 1980; Sillett et al., 2000; Ahola et al., 2004; Stenseth & Mysterud, 2005; Macmynowski et al., 2007). Unprecedented increases in global temperatures (IPCC, 2001) have altered migratory phenology for a

Correspondence: Anna M. Calvert, Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4J1, e-mail: anna.calvert@dal.ca

variety of organisms (e.g. Roy & Sparks, 2000; Weishampel *et al.*, 2004; Marra *et al.*, 2005; Gordo & Sanz, 2006), and have been linked to ensuing survival and reproductive declines (Stevenson & Bryant, 2000; Thomas *et al.*, 2001; Visser *et al.*, 2004). Nevertheless, response to climatic shifts is likely to vary with migratory distance or strategy (Forchhammer *et al.*, 2002; Rivalan *et al.*, 2007), and thus migrants may differ in their vulnerability to future global change.

Small-scale daily migratory movements by passerine birds are affected by local weather, as migrants attempt to reduce environmentally induced flight costs (such as those caused by strong head-winds, cold temperatures or precipitation) by varying the timing and duration of *en route* stopovers (Richardson, 1990; Weber *et al.*, 1998a; Åkesson & Hedenström, 2000; Danhardt & Lindström, 2001). Stopovers provide migrants an opportunity both to rest and replenish energetic stores and to wait for favourable flight conditions, particularly before travel across geographical barriers (e.g. flight over open ocean; Alerstam, 1979; Bruderer & Liechti, 1998), yet the use of stopovers also incurs significant time and energy costs (Wikelski *et al.*, 2003). Under optimal migration, stopover decisions will reflect trade-offs between the need for fuel accumulation, the costs of feeding and fuel transport, and the risks of mortality or misorientation associated with flying in dangerous weather conditions (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992; Hedenström & Alerstam, 1997). Variation in use, duration and timing of stopovers in response to weather is thus likely to also depend on bird condition (i.e. fuel-load) (Weber *et al.*, 1998b; Danhardt & Lindström, 2001; Wikelski *et al.*, 2003; Macmynowski *et al.*, 2007).

Individual marking of avian migrants, often used for assessing population trends and tracking migratory routes, can also be used to obtain detailed insight into decisions made by migrants during stopover through the application of recent modifications to mark–recapture methods (Lebreton *et al.*, 1992; Schaub & Jenni, 2001; Schaub *et al.*, 2001). In particular, the multistate model proposed by Schaub *et al.* (2004) permits estimation of the probability that a bird arriving at a stopover site will leave again within 24 h of arrival (a 'transient') or will stopover for at least a day ('non-transient'). It also provides for the estimation of the daily probability of departure (and therefore, duration of stay) for birds that do stopover. Whether to stopover for refuelling, and how long to stay at a particular site, are key decisions that affect the condition of the individual during migration and the timing of arrival.

In this paper, we use mist-netting data from a coastal stopover site in Atlantic Canada to assess how variation in an intrinsic factor (fuel-load) and extrinsic factors at two scales (weather, climate) influences whether pas-

serines stopped over to refuel at the site (transience) and how long they stayed (departure). We applied the model of Schaub *et al.* (2004) to (1) characterize interannual variation in probabilities of transience and departure by three species groups of autumn passerine migrants over 12 years, and (2) determine how migratory fuel-load may interact with both local weather conditions and broader regional climatic patterns to drive temporal patterns of stopover behaviour.

Methods

Study system

Data were collected at the Atlantic Bird Observatory's long-term netting site on Bon Portage Island (BP), Nova Scotia (43°28′N, 65°44′W) as part of the Canadian Migration Monitoring Network (CMMN). Autumn migration monitoring has been conducted annually from mid-August to the end of October since 1996. Most passerine species migrating through this region cross the Gulf of Maine following autumn stopover in Nova Scotia (Richardson, 1972; Williams *et al.*, 1977).

Every day during the migration-monitoring season (except in extreme weather), up to 15 fixed-location mist nets (12 m × 2.6 m, four panel, 36 mm extended mesh) were unfurled 30 min before sunrise, and checked every 30 min for up to 6 h; nets were visited more frequently and/or closed early in inclement weather, and the total daily net-minutes were recorded. All passerines captured were marked with individually coded standard USFWS/CWS metal leg bands. Age and sex were determined when possible from morphological characters according to Pyle (1997), migratory fat-load was assessed, and birds were measured and weighed before release. All recaptures (same or different day) were recorded.

Analyses focused on migratory warblers and sparrows, which are captured regularly at BP during their nocturnal autumn migration through eastern North America. We used data for hatch year (HY; i.e. young-of-the-year on their first southward migration) birds only, given that they made up 93% and 91% of known-age autumn captures at BP for warblers and sparrows, respectively. Sexes were not separated for analysis: most HY birds could not be sexed, and other studies indicate little sex differentiation in passerine stopover behaviour (Hussell, 1981; Morris *et al.*, 1996). The autumn migration season was defined as beginning in late August, to avoid inclusion of local breeders.

The temporal distribution of warbler captures over the migration season was bimodal, with clear early- and late-autumn peaks. Additionally, the two waves of warblers had distinct species assemblages that were

consistent from year to year. The 'early warbler' wave was dominated by four species, in roughly equal proportions: American redstart (*Setophaga ruticilla*), black-and-white warbler (*Mniotilta varia*), common yellowthroat (*Geothlypis trichas*) and northern waterthrush (*Seiurus noveboracensis*). Given that all other warbler species were rarely observed during the early time period, we included only these four dominant species in our group (see Appendix A). The 'late warbler' wave was dominated (ranging from 43% to 86% of late fall captures every year) by a single species, the yellow-rumped warbler (*Dendroica coronata coronata*), and no other species made up more than 6% of the late warbler total. We used only this species in our late-warbler analysis, as the behaviours of other species would likely be masked by the prevalence of yellow-rumped warblers. The blackpoll warbler (*Dendroica striata*) has a unique transoceanic autumn migration with specialized stopover behaviour (Nisbet *et al.*, 1995; Hunt & Eliason, 1999), and was excluded from analyses.

The breeding and wintering range of the later migrating, yellow-rumped warbler extends further north than those of most early warbler species (Brewer *et al.*, 2000; Dunn *et al.*, 2006), such that the early migrants generally have a greater remaining migratory distance following stopover at BP. We, therefore, considered the early warbler group to represent longer-distance migrants, and the late (i.e. yellow-rumped) warblers to be representative of medium-distance migrants. Although individual species will differ in some details of their stopover behaviour (Morris *et al.*, 1996), the grouped species might be expected to respond in broadly similar ways to environmental factors, as they migrate at the same time of year (and thus experience the same weather conditions), rely upon the same general food sources (primarily insects, supplemented with fruits or seeds), and follow similar autumn migration routes (down the Atlantic coast, from breeding grounds in NE Canada to winter in the Gulf of Mexico, Central/South America; Brewer *et al.*, 2000; Dunn *et al.*, 2006).

Sparrow species were similarly pooled, including only late-autumn captures (after mid-September) to exclude any local breeders. The most frequently captured species were the white-throated sparrow (*Zonotrichia albicollis*), song sparrow (*Melospiza melodia*), swamp sparrow (*Melospiza georgiana*) and slate-coloured (dark-eyed) junco (*Junco hyemalis*), and therefore we restricted our sparrow group to only these four species (Appendix A). These species are also broadly similar to one another, with seed-dominated diets and a more northerly wintering ground than most warblers (midlatitude USA to Mexico; Brewer *et al.*, 2000), thus representing short-distance migrants. Although pooling data among species likely obscures some details of the migratory strategies of particular species, it gives us additional power to answer questions of large-scale climatic influence more generally, for groups of species with comparable migratory strategies.

Fuel-load index

Fuel-load was determined by visual inspection of the furculum (interclavicular depression), breast and abdomen at the time of first capture of an individual, and each migrant was assigned a fat score based on a multilevel categorical fat index (a modification of the Kaiser (1993) index). Individual fat-load at first capture should be directly relevant to stopover decisions in migrants whose departure depends upon stored fuel (Alerstam & Lindström, 1990), as fat is the main fuel source for migrants and can be accumulated and metabolized quickly (Bairlein, 1990; Ramenofsky, 1990; McWilliams *et al.*, 2004). The fat index values were grouped into two categories for the analyses: 'high-fat' individuals were all those whose furculum was at least half-full of fat at first capture, and included migrants carrying additional fat under breast and abdominal feathers and below the wings; 'low-fat' individuals were those whose furculum was less than half-full of fat (or empty) at first capture (Rogers, 1991; Kaiser, 1993).

Quantification of stopover behaviours

During migration over land, nocturnally migrating passerines typically leave a site after sunset, fly for part of the night and land before sunrise. When a migrant lands, it must decide whether to remain on that site and refuel for a later flight (i.e. to stopover for 1 day or more), or whether to take off again the next evening to search for a more favourable site (i.e. to be transient; Alerstam & Lindström, 1990; Weber *et al.*, 1999; Dunn, 2002). If it does remain to refuel, a migrant must then decide on which day to leave. As defined by Schaub *et al.* (2004), transients are those birds that have a departure probability of 1 on the evening after arrival (they depart within 24 h, likely the following night, and are assumed to have continued migrating or to have moved to a different site). Nontransients are those that stay >24 h, and thus have the potential to be recaptured (Schaub *et al.*, 2004).

These decisions can be cast in a multistate mark–recapture model framework, with an initial state (first capture only), a transient state (departure within 24 h preventing recapture and thus unobservable) and a nontransient state (potential for subsequent recapture). The proportion of transients is estimated from the matrix transition probability from the initial to transient

state, while departure probabilities are estimated from daily 'survival' probabilities in the nontransient state (see Schaub *et al.* (2004) for transition matrix and parameter vectors); variation in daily recapture probability between states can also be estimated. We used these multistate mark–recapture models to estimate (i) the daily proportion of transients (τ) among newly banded birds, (ii) the daily probability of recapturing a nontransient bird present at the site (p) and (iii) the daily departure probability (ε) of nontransient birds (Schaub *et al.*, 2004). Note that daily 'survival' ($1-\varepsilon$) was directly estimated in the models, but for simplicity we present only ε values.

We built a separate set of candidate multistate models for each species-group/year combination from 1996 to 2007 (three species-groups over 12 years: 36 model sets). Each model set was based on data from an 18–35 day (mean 31 days) period of mark and recapture records corresponding to peak autumn migration: this ranged from 19 September to 24 October for sparrows, 22 August to 26 September for early warblers and 26 September to 31 October for late warblers. We did not analyse species-year combinations where fewer than 70 birds were banded during the time period, eliminating six model sets (sparrows: 1996, 2004, 2005, 2006; late warblers: 2004, 2005).

Each model set began with a general model allowing an interaction of fat-load effect and daily variation on ε and p, and a fat-load effect on τ {$\varepsilon_{\text{fat}\times t} \, p_{\text{fat}\times t} \, \tau_{\text{fat}}$}. We then built a series of biologically reasonable reduced models, wherein ε, p and τ could vary with individual fat-load (low vs. high fat: ε_{fat}, p_{fat}, τ_{fat}); we also allowed recapture rate to be fat-invariant (p), but built only fat-variant models of ε and τ given our interest in quantifying the role of fat-load on stopover decisions. In addition, p could vary with netting effort (total daily net-minutes), and was fixed at 0 on days where nets were not opened. This fixing of p applied regardless of constraints imposed, such that only days with nets open were modelled as a function of time or netting effort. Finally, ε was also allowed to vary linearly across days within a season. Initial results served as the basis for subsequent candidate models.

Inferences regarding models that best described the data were based on the Akaike Information Criterion (AIC), which represents a trade-off between model complexity and bias (Akaike, 1973). For each model set, goodness-of-fit of the general model to the data was estimated with bootstrap methods in program MARK (White & Burnham, 1999). The resulting variance inflation factor ($\hat{c}$; Lebreton *et al.*, 1992) was used to correct for data overdispersion by adjusting deviance in the AIC$_c$ (sample size-adjusted AIC) calculation to become QAIC$_c$ (quasi-likelihood AIC$_c$), and models were ranked by QAIC$_c$ value (smaller QAIC$_c$ indicating greater parsimony; Burnham & Anderson, 2002). Parameters were estimated by maximum likelihood with a logit link in MARK (White & Burnham, 1999). Relative (Δ) QAICc values were used to compare models, and the importance of specific factors (linear ε trend across days; daily effort constraint on p) was additionally based upon effect size confidence intervals. Initial modelling provided little support for daily time-variance of departure in any dataset (Table 1), so time-invariant estimates of ε were used in modelling of interannual variation.

Weather and climate data

Climatic effects operate at different spatial and temporal scales from local weather (Stenseth *et al.*, 2003; Hallett *et al.*, 2004; Stenseth & Mysterud, 2005). One of our objectives was, therefore, to determine how well local weather or climatic factors could predict interannual variation in stopover behaviour of the three passerine groups. Local weather conditions were based on surface-level meteorological measurements near the stopover site (Yarmouth, NS, $\sim$45 km northwest of BP) at the time of day when migrants would likely make departure decisions ($\sim$ sunset to midnight; Martin, 1990; Peckford & Taylor, 2008). Relevant weather variables (wind speed, precipitation: Richardson, 1990; Pyle *et al.*, 1993; Åkesson & Hedenström, 2000; Schaub *et al.*, 2004) were extracted from hourly records obtained from Environment Canada (Meteorological Service of Canada); the role of head- vs. tail-winds was not examined because of potentially contrasting orientation directions among individual migrants originating from different breeding locations (Fitzgerald & Taylor, 2008). Average conditions were calculated for 18:00–24:00 hours of each evening between netting days.

The North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) indices are frequently used as measures of longer-term and larger-scale climatic fluctuations (Hurrell *et al.*, 2003; Stenseth *et al.*, 2003). We used the NAO index of the previous winter (based on the Iceland–Azores pressure differential in the Atlantic) as an annual index of variation in conditions both on migrants' wintering and breeding areas. A positive winter NAO correlates with warm, wet conditions in the southern USA and Gulf of Mexico (i.e. wintering grounds for many migrants) but with cool, dry conditions in eastern Canada (i.e. breeding grounds; Hurrell, 1995; Visbeck *et al.*, 2001). The ENSO index, based on sea surface temperatures in the tropical Pacific Ocean, is generally associated with warming ('El Niño', positive values) and cooling ('La Niña', negative values), as well as variation in precipitation, in Central and South America (Timmermann *et al.*, 1999; Stenseth

Table 1 Summary of data for multistate mark–recapture for autumn passerine migrants at Bon Portage Island, Nova Scotia, including time-periods and sample sizes, as well as the relative importance of a linear time constraint on daily departure probability (ε) and of a fat-load constraint on daily recapture probability (p) as tested within the program MARK

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
Early warblers												
Encounter days	August 22–September 24	August 23–September 26	August 23–September 25	August 23–September 26	August 23–September 26	August 23–September 26	August 23–September 26	August 24–September 26	August 22–September 25	August 23–September 25	August 23–September 26	August 23–September 26
Number birds banded	339	150	226	218	254	460	214	248	182	159	239	160
Fat effect on p (low-fat)	ns	ns	(+)	ns	ns	ns	ns	ns	ns	(+)	ns	ns
Linear (daily) trend in ε	ns	ns	ns	ns	ns	ns	ns	ns	ns	(+)	ns	ns
Late warblers												
Encounter days	September 26–October 13	October 2–October 23	September 23–October 24	September 27–October 28	September 27–October 28	September 20–October 23	September 28–October 25	September 30–October 31	NA	NA	September 30–October 27	September 29–October 25
Number birds banded	222	220	172	579	507	346	369	134	NA	NA	187	210
Fat effect on p (low-fat)	ns	ns	(+)	ns	ns	ns	ns	ns	NA	NA	ns	ns
Linear (daily) trend in ε	ns	ns	ns	ns	ns	ns	ns	ns	NA	NA	ns	ns
Sparrows												
Encounter days	NA	September 23–October 23	September 23–October 24	September 20–October 22	September 24–October 23	September 19–October 23	September 23–October 24	September 20–October 20	NA	NA	NA	September 24–October 19
Number banded birds	NA	318	147	93	188	179	75	87	NA	NA	NA	109
Fat effect on p (low-fat)	NA	ns	ns	ns	ns	ns	ns	ns	NA	NA	NA	(–)
Linear (daily) trend in ε	NA	ns	ns	ns	ns	ns	(+)	ns	NA	NA	NA	Ns

Significant effects (95% CI on β not including 0) are noted by ($+$) or ($-$) for positive or negative effects, respectively, of low fat-load or day within the migration season; nonsignificant effects are indicated as 'ns'. Insufficient data for sparrows in 1996, 2004, 2005, and 2006, and for late warblers in 2004 and 2005, precluded analysis of those migrations.

et al., 2003). The ENSO index from the previous winter could thus reflect climatic conditions in the overwintering locations of North American migrants. Climatic conditions during the previous winter would be relevant to subsequent autumn migration if they affect summer conditions (e.g. food availability) during breeding in the northern hemisphere, or if there are carry-over effects on fitness from conditions on the wintering grounds (Marra *et al.*, 1998; Bearhop *et al.*, 2004; Mazerolle *et al.*, 2005).

Mixed-effects models

Constraints within MARK (White & Burnham, 1999) on the complexity of model structure limit its uses in the analysis of parameter variation across multiple scales. For instance, 'robust design' models permit stratification of survivorship into primary and secondary sampling intervals (e.g. year and day, respectively), but short-term survivorship among secondary periods is not estimable, and the multistate extension of the robust design model does not allow for state-transitions within primary sampling periods (Kendall *et al.*, 1995; White *et al.*, 2006). Consequently, the use of MARK (White & Burnham, 1999) alone to model annual variation in stopover parameters estimated from daily encounters using the multistate model structure described above would be structurally cumbersome (requiring the analysis to be partitioned among 72 'groups') and logistically complex. We therefore used a two-step approach, applying MARK (White & Burnham, 1999) to estimate annual values for daily behavioural parameters (transience, departure) by fat-load based on a daily-invariant model, and then fitting linear mixed-effects models to link interannual variation in daily stopover behaviour to environmental variables.

The response variables used in the mixed-effects analysis were mean annual fat-dependent parameter estimates (ε_{fat} and τ_{fat}) from model $\{\varepsilon_{fat}\,p_{effort}\,\tau_{fat}\}$. Data points were not included if they were estimated at exactly 0 or 1 (indicating inestimable parameters due to small sample sizes; a total of 9/60 data points were eliminated in the departure analyses, and 14/60 points in the transience analyses). Models were built using the 'lmer' function in program R (version 2.7.0; R Development Core Team, 2008), with a logit-link to allow for logistic transformation of the response variable (ε or τ) given that it was bounded by 0 and 1; the 'quasi' model family allowed logistic transformation with normal error distribution. Each departure or transient probability was weighted by the number of banded birds upon which the estimate was based, to account for potentially large variation of small-sample estimates, and thus reduce bias from estimation error. To account for inter-

dependence among data points from a given year due to common environmental influences, *year* was included in all models as a random-effect; fat-load, species-group and weather/climatic indices were all treated as fixed effects. The full model included all environmental variables (verified for correlation) with no interactions; reduced models were fit with stepwise backward elimination based on quality of parameter estimates and contributions of terms to model fit, but all models included year-specific intercepts. Models with variable weather effects by fat-load or species-group (i.e. interactions between categorical and continuous fixed-effects) for all remaining environmental variables were then tested one by one.

Predictor variables included in the full model for both departure and transient probabilities were (in order of inclusion): *fat-load* (categorical: low vs. high fat-load at first capture), *species group* (categorical: early warblers, late warblers, sparrows), *NAO* (NAO index from previous December–March), *ENSO* (ENSO index from previous December–February), *wind speed* (proportion of nights with average wind speed $>10\,km\,h^{-1}$) and *precipitation* (proportion of nights with fog or rain on $>50\%$ of hourly evening observations).

Results

Estimates of transience, departures and stopover duration

The number of banded migrants per year in datasets for multistate models averaged 237 for early warblers (range 150–460), 295 (134–579) for late warblers and 149 (75–318) for sparrows (Table 1). Between 0.6–11.5% (mean 5.8%) of captured migrants were recaptured at least once. Except for two datasets, over-dispersion values were all $\hat{c} < 2.5$ (most close to $\hat{c} = 1$), suggesting good fit of general models to the data (Burnham & Anderson, 2002); $\hat{c}$ values were used to adjust deviance calculations and estimation errors.

Effort-constrained models (those including netting time, p_{effort}) always performed better than models with time-variant p, and fat-load effects on p (p_{fat}) were rarely significant (Table 1); consequently, all subsequent models were built with the p_{effort} constraint. Mean daily recapture probabilities from model $\{\varepsilon_{fat}\,p_{effort}\,\tau_{fat}\}$ averaged 10.0% per 90 net-hours (i.e. all 15 nets open for 6 h daily) across the 30 model sets. There was little support for linear trends in daily departure probability within years (Table 1). We subsequently built only models where departure and transience were constant across days and differed among fat groups (ε_{fat} and τ_{fat}), because of our interest in modelling fat-specific variation in among years.

For each species group, time- and fat-invariant estimates of transience and departure were estimated for
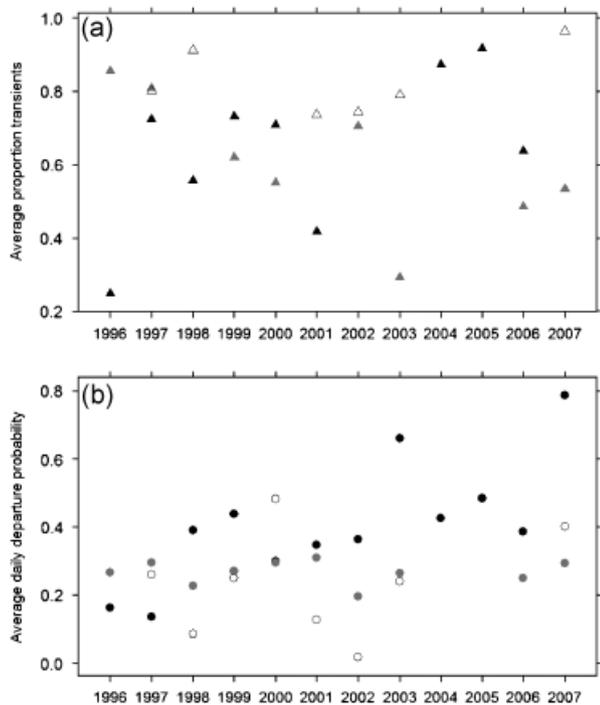
Fig. 1 (a) Average proportion of transient migrants for early warblers (black triangles), late warblers (grey triangles), and sparrows (white triangles) migrating through Bon Portage Island (BP), Nova Scotia, during autumn 1996–2007. (b) Average daily departure probability for early-migrating warblers (black circles), late-migrating warblers (grey circles), and sparrows (white circles) at BP during autumn 1996–2007. Estimates from model $\{\varepsilon.\ p_{effort}\ \tau.\}$; boundary estimates (0 or 1) are not shown.

each year from model $\{\varepsilon.\ p_{effort}\ \tau.\}$. The proportion of transient migrants at BP was highly variable over time, with some indication of a decreasing temporal trend for all three species groups between 1996 and 2001 (Fig. 1). Average departure probabilities also varied among years, particularly in early warblers that showed an overall increase in departure probability (i.e. shorter stopover duration) over the 12 years studied; sparrows and late warblers generally had lower departure probabilities than early warblers (Fig. 1). The formula $[-1/\ln(1-\varepsilon)]$ can be used to estimate stopover duration (Schaub *et al.*, 2001), indicating that early warblers stopped for 1–7 days at BP, while late warblers stopped for 3–5 days and sparrows 2–60 days.

Environmental variables and migratory fuel-load

Variation in the stopover behaviour of passerines at BP was significantly related to variation in both broad-scale climatic factors and in local weather patterns (Tables 2 and 3). The proportion of birds that were transient (stayed less than a day) was higher in years with a positive NAO index (particularly in early warblers and sparrows; Fig. 2a) or a positive ENSO index (for sparrows only; nonsignificant ENSO effect for warblers; Fig. 2b) in the previous winter. The proportion of late warblers that were transient was also higher in years with less frequent precipitation during the migration season (Fig. 2c, Table 3). Departure probability varied

Table 2 The five best-fit linear-mixed-effects models (with the best model in bold) representing interannual variation in the proportion of transients (τ) and daily departure probability (ε) of autumn songbird migrants captured at Bon Portage Island, NS, Canada from 1996 to 2007, as well as the number of parameters, deviance, and ΔAIC value for each model

Model	# Parameters	Deviance	ΔAIC
Proportion transients (τ)			
species + NAO + ENSO + precip + (1 | year) + species:precip + species:ENSO	**11**	**112.00**	**0.00**
species + NAO + ENSO + highwind + precip + (1 | year) + species:precip + species:ENSO	12	110.50	0.50
species + NAO + ENSO + highwind + precip + (1 | year) + species:precip + species:ENSO + species:NAO	14	107.30	1.30
fat + species + NAO + ENSO + precip + (1 | year) + species:precip + species:ENSO	12	111.30	1.30
species + NAO + ENSO + highwind + precip + (1 | year) + species:precip + species:NAO	12	117.80	7.80
Departure probability (ε)			
fat + species + NAO + highwind + precip + (1 | year) + fat:NAO	**9**	**65.66**	**0.00**
fat + species + NAO + highwind + precip + (1 | year) + fat:wind	9	66.14	0.48
fat + species + NAO + ENSO + highwind + precip + (1 | year)	9	67.08	1.42
fat + species + NAO + highwind + precip + (1 | year)	8	69.83	2.17
fat + species + NAO + precip + (1 | year) + fat:NAO	8	70.36	2.70

Categorical fixed-effects were fat (low vs. high migratory fuel-load) and species (early warblers, late warblers, sparrows); environmental variables included in candidate models were NAO (North Atlantic Oscillation index from previous December to March), ENSO (El Niño Southern Oscillation index from previous December to February), wind speed (proportion of nights with average wind speed $> 10\,\mathrm{km\,h^{-1}}$), and precipitation (proportion of nights with fog or rain on $> 50\%$ of hourly evening observations). Random-effects variation among years is indicated as (1 | year), while differences in slope of environmental effects among species- or fat-groups are indicated by, for example, species : precipitation.

Table 3 Final linear mixed-effects models selected as the best representation of interannual variation in transience and departure probability of migratory passerine stopovers at Bon Portage Island, Nova Scotia, in autumn 1996–2007; effects are derived from the models shown in bold in Table 2

Variable	Effect size (logistic)		
Proportion transients (τ)			
'fixed' effects	Beta	SE	95% CI
(Intercept)	0.26	0.90	(−1.50, 2.02)
Species group	Late warblers: 3.50	1.34	(0.87, 6.13)
	Sparrows: 2.42	1.50	(−0.52, 5.36)
NAO index	0.29	0.11	(0.07, 0.51)
ENSO index	−0.05	0.19	(−0.42, 0.32)
Species : ENSO	Late warblers: 0.09	0.23	(−0.36, 0.54)
	Sparrows: 5.98	2.25	(1.57, 10.4)
Precipitation	0.17	2.46	(−4.65, 4.99)
Species : precipitation	Late warblers: −18.44	5.47	(−29.2, −7.72)
	Sparrows: 11.06	7.20	(−3.05, 25.2)
'random' effect	Variance	SE	
Year	Year: 0.33	0.57	
	Residual: 2.09	1.45	
Departure probability (ε)			
'fixed' effects	Beta	SE	95% CI
(Intercept)	1.38	0.42	(0.56, 2.20)
Fat group	Low-fat: −0.41	0.14	(−0.68, −0.14)
Species group	Late warblers: −0.89	0.21	(−1.30, −0.48)
	Sparrows: −0.94	0.26	(−1.45, −0.43)
NAO index	0.003	0.05	(−0.09, 0.10)
Fat : NAO	Low-fat: 0.13	0.07	(0.01, 0.27)
Wind speed	−1.15	0.56	(−2.25, −0.05)
Precipitation	−2.57	0.96	(−4.45, −0.69)
'random' effect	Variance	SE	
Year	Year: <0.001	<0.001	
	Residual: 1.26	1.12	

Important environmental predictor variables (based on stepwise backward elimination and AIC) are shown with logistic-transformed effect sizes (Beta), standard errors (SE) and 95% confidence interval for fixed effects (Beta ± 1.96SE); fat and species effects are shown relative to high-fat and early-warbler groups, respectively. Variation attributable to 'random' year effect is the difference in intercept relative to baseline model values.
NAO, North Atlantic Oscillation; ENSO, El Niño Southern Oscillation.

with the winter NAO index, and with precipitation and wind speed during the migration season, and responses did not vary significantly among species groups (Tables 2 and 3, Fig. 3). Birds departed sooner in years preceded by a high winter NAO (Fig. 3a), years with low winds (Fig. 3b) or years with infrequent precipitation (Fig. 3c).

The proportion of birds that were transient did not vary with fat-load, nor did the relationships between transience and the environmental influences (Tables 2 and 3). This suggests that decisions made by migrants immediately upon arrival are relatively independent of current fuel stores. There was, however, strong support for greater daily departure probabilities (i.e. shorter stopover duration) among high- than low-fat birds, and for a stronger NAO effect on low-fat than high-fat birds (Table 2, Fig. 3). Fat level had little or no effect on

the relationships between departure probability and precipitation or wind-speed. Thus, though high-fat birds had a greater tendency for early departure, the two fat groups responded in very similar ways to environmental influences when making departure decisions.

Discussion

Before we can begin to project the consequences of climatic shifts on populations we must understand how the current environment influences population dynamics, including effects on different life cycle stages (Adahl *et al.*, 2006). Environmental factors are relevant to long-distance migrants at multiple temporal and geographic scales, due to use of geographically and
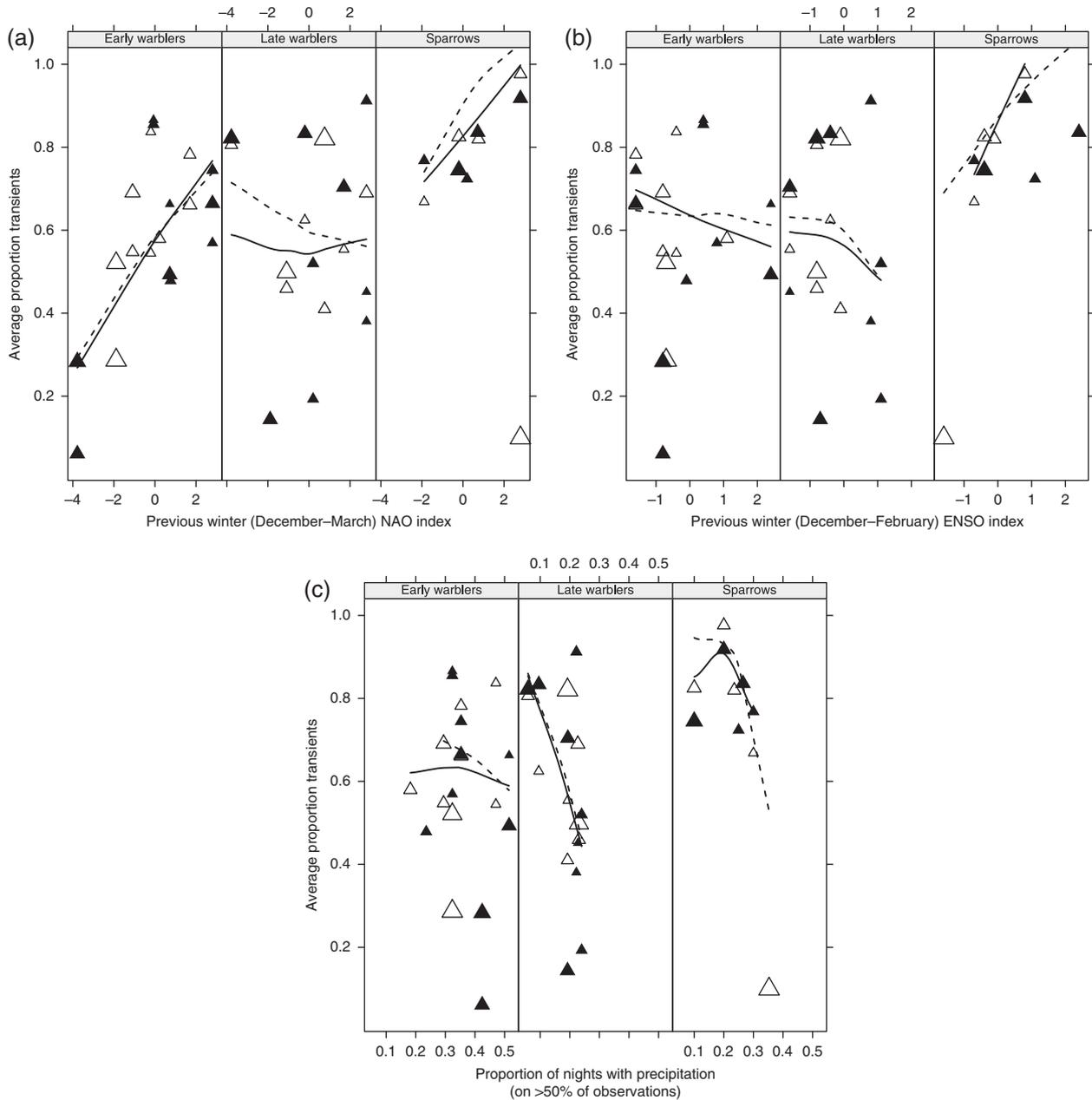
Fig. 2 Variation in annual average proportion of autumn-migrating passerines that were transient at Bon Portage Island, 1996–2007, for high-fat (black, solid line) and low-fat (white, dashed line) birds, relative to North Atlantic Oscillation (NAO) index the previous winter (a), El Niño Southern Oscillation (ENSO) index the previous winter (b), and the frequency of nights with precipitation (c); point size is log-scaled according to sample size (i.e. the number of birds banded); fitted relationships shown are from the linear mixed-effects model described in Table 2.

climatically separated habitats (e.g. Crozier & Zabel, 2006; Macmynowski *et al.*, 2007), and because conditions during one season may affect fitness in subsequent seasons (Bearhop *et al.*, 2004; Visser *et al.*, 2004; Lehikoinen *et al.*, 2006). As a step toward understanding potential impacts of future climate change upon the persistence of migratory passerines, we demonstrated important links between autumn stopover behaviour and both

local weather and regional climatic indices. Further, while studies of migration propensity or timing have showed that responses to climate may differ with migratory strategy (Rivalan *et al.*, 2007) or migration distance (Jenni & Kéry, 2003), we found similar stopover–environment relationships across diverse passerine groups. Our results suggest, therefore, that there may be parallel impacts of weather and climate
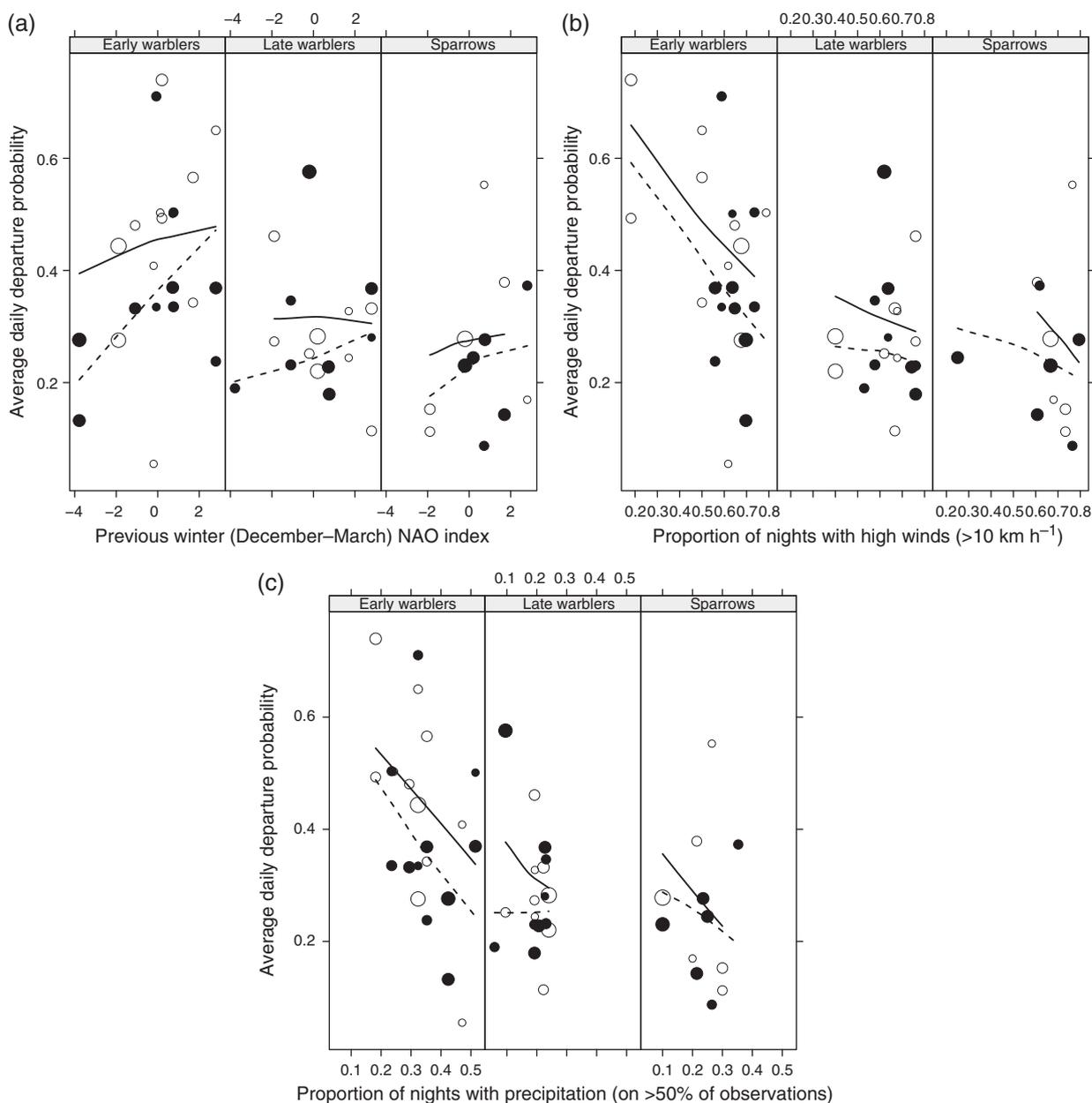
Fig. 3 Variation in average daily departure probability of autumn-migrating warblers and sparrows at Bon Portage Island, 1996–2007, for high-fat (black, solid line) and low-fat (white, dashed line) birds, relative to North Atlantic Oscillation (NAO) index the previous winter (a), the frequency of nights with high wind speeds (b), and the frequency of nights with precipitation (c); point size is log-scaled according to sample size (i.e. the number of birds banded); fitted relationships shown are from the linear mixed-effects model described in Table 2.

on diverse passerines using a particular stopover site.

Temporal variation in stopover behaviour

Average daily departure probabilities of autumn migrants varied between ~2% and 50% across the three species groups, with an overall increase in departure probability over the time period 1996–2007 ob-

served for the longest-migrating group, the early warblers. In contrast, the proportion of transients (staying <24 h) fluctuated greatly over the 12-year period in all three species groups, with some indication of a decline until 2001 and then resurgence. Thus, autumn use of BP as a typical stopover (i.e. for refuelling; Alerstam & Lindström, 1990) appears to be highly variable from year to year; in some years fewer than 10% of migrants landing at BP remained for more than a

day. To our knowledge, this is the first quantification of such fluctuating and often limited stopover use by a large and varied group of migrants.

There was little support for any linear change in daily departure probability within a season, suggesting that seasonal time constraints were of minor importance relative to fat-load and environmental influences. A study of decision-making during spring when migration timing is critical to reproductive success (Møller, 1994; Drent *et al.*, 2003), however, might produce quite different results.

Environmental influences on stopover decisions

Migrants may be affected by environmental factors at several scales (e.g. Frederiksen *et al.*, 2004; Macmynowski *et al.*, 2007). At the scale of the island of BP, we focussed on the interannual variability of two important local weather features (wind speed and precipitation) that were expected to affect the ability or willingness of migrants to cross the Gulf of Maine following stopover, and found that both weather components were linked to stopover behaviour. Migrants were more likely to stopover at BP (i.e. to be less transient; late warblers only), and stopped over for longer (i.e. showed lower departure probabilities), in years of frequent precipitation, supporting evidence from other studies that migration can be impeded by rain or fog (Pyle *et al.*, 1993; Åkesson *et al.*, 2001; Schaub *et al.*, 2004). Additionally, the negative effects of precipitation and wind speed on departure were most evident in the further-travelling warblers relative to shorter-distance sparrow migrants, consistent with theory suggesting that stopover constraints may be particularly critical to long-distance migrants (Alerstam & Lindström, 1990; Hedenström & Alerstam, 1997). Departure occurred sooner, on average, in years of low winds, also consistent with evidence that migrants prefer to fly on calm nights (Richardson, 1990; Pyle *et al.*, 1993; Danhardt & Lindström, 2001).

Recent projections point to probable increases in both precipitation and wind with future climate shifts (Easterling *et al.*, 2000; Hurrell *et al.*, 2003), suggesting that increased use of sites like BP may occur in the future, with possible implications for the number of days birds spend *en route* to their wintering grounds. While past studies have shown that daily weather influences daily variation in stopover behaviour, our results demonstrate that environmental conditions important on a daily basis also scale up to produce differences in average behaviour among years. An important next step would be to determine the extent to which lifetime fitness is affected by this degree of variation in migratory behaviour.

The NAO has been implicated in several aspects of migration variability, including changing phenology (Forchhammer *et al.*, 2002; Huppop & Huppop, 2003; Vahatalo *et al.*, 2004), altered food availability on breeding grounds (Frederiksen *et al.*, 2004) and consequent variation in survival or reproductive success (Przybylo *et al.*, 2000; Sanz, 2003; Sandvik *et al.*, 2005; Crespin *et al.*, 2006); the ENSO has similar far-reaching implications for migration (e.g. Stenseth *et al.*, 2003; Sedinger *et al.*, 2006; Macmynowski *et al.*, 2007). Our results suggest that the autumn stopover behaviour of juvenile passerines may be influenced by climatic processes affecting their parents' wintering ground conditions in the previous year. Transience was higher, and stopover duration shorter, for all three species groups of autumn migrants in years following positive NAO winters, which are characterized by warm, wet weather in the wintering areas for most of the species in our analysis (southeastern US, Caribbean, Central America) but cold, dry winters in northern Canada (Hurrell, 1995; Visbeck *et al.*, 2001). This suggests that the pattern is more likely due to the effect of the NAO on winter parental fitness than on spring food production on the breeding grounds; the absence of correlations between winter NAO and local spring/summer weather (temperature, precipitation; all $P < 0.05$, $R^2 < 0.10$; A. Calvert, unpublished data) further discounts a direct NAO influence upon breeding season weather. The higher transience of sparrows in years of positive ENSO indices, following warm 'El Niño' conditions on wintering grounds, also supports positive effects of climate in the nonbreeding season. Given the growing evidence for carry-over of winter climatic impacts into subsequent reproduction (Marra *et al.*, 1998; Bearhop *et al.*, 2004; Mazerolle *et al.*, 2005), it is plausible that warm winters might result in the production of healthier HY birds – requiring less resting/fuelling, and thus higher transience and shorter stopovers, during their southward migration (Przybylo *et al.*, 2000; Sanz, 2003; Weatherhead, 2005).

The global climate is undergoing rapid transformation, with positive-value phases of both the NAO and ENSO expected to become more frequent (Timmermann *et al.*, 1999; IPCC, 2001; Visbeck *et al.*, 2001). Consequently, in addition to other anticipated migratory impacts of NAO and ENSO variation (e.g. Sillett *et al.*, 2000; Forchhammer *et al.*, 2002; Sedinger *et al.*, 2006) the sensitivity of both transience and departures to broad climatic patterns could result in shorter autumn stopovers of passerines at locations such as BP. However, the inclusion of local weather effects makes predictions more complex, as the increased wind and precipitation expected from future climatic shifts would tend to lower transience and departure probabilities.

Given that broad-scale climatic effects such as the NAO and ENSO operate over long time-frames, the influences detected over this 12-year period should be viewed as a starting point for further investigation.

While the pooling of multiple species into generalized groups inevitably obscures species differences in behaviour, it permits a comparison of stopover decisions among birds differing in the timing and distance of migration. The generally consistent effects of particular environmental factors on stopover behaviour across the three species groups suggest a common response to important variables such as rain (though not for transience), wind, and climatic variation that influences conditions on the wintering grounds. Consistent species composition within groups among years (Appendix A) further indicates that interannual fluctuations in behaviour were not driven by changing species dominance over time. Our results thus imply that the species using BP as an autumn stopover show broadly similar sensitivities to environmental factors. As more robust modelling tools are developed, finer-scale analysis may enable us to determine species-specific stopover behaviours and responses to environmental change, as was possible here for only Yellow-rumped warblers.

Importance of migratory fuel-load

Fat-load can indicate the individual preparedness for flight of each migrant (Bairlein, 1990; Ramenofsky, 1990), and thus was expected to influence migratory behaviour. Stopover behaviour of migrants at BP was at least somewhat consistent with a time-minimizing strategy (Alerstam & Lindström, 1990; Lindström & Alerstam, 1992): departure probabilities were higher, and therefore stopover durations shorter, for migrants with high fat-loads than for lean migrants. Moreover, there was additional evidence to support steeper relationships of daily departure probability to the NAO in low-fat than high-fat migrants, suggesting potentially stronger sensitivity of lean individuals to environmental influences. In contrast, neither the proportion of transients nor its dependence upon environmental variables was linked to fat-load. Taken together, these results suggest that decisions made by migrants upon arrival at a potential stopover (i.e. transience) are initially weather- and climate-driven, but then that subsequent stopover decisions (i.e. stopover duration and timing of departure) respond to a combination of metabolic constraints (fat-load) and environmental influences at both local and regional scales.

Conclusions and implications

We expected variable weather and fat-load responses by different migrants, as a reflection of trade-offs among temporal, energetic, and predation pressures (Ydenberg et al., 2002; Drent et al., 2003; Prop et al., 2003) and differences in migratory timing, distance, or strategy (Alerstam & Lindström, 1990). However, similar environmental factors appeared relevant to all three species groups, with some differences in the strength but not direction of responses. Lean birds showed lower departure probabilities and were slightly more sensitive to environmental conditions, but fat-load did not affect the direction of behavioural responses, and patterns of interannual variability in behaviour were very similar. Thus, our results point toward a multiscale process of environmental influence that may be broadly applicable to all autumn passerine migrants, where (1) winter climatic conditions influence parental physical condition and thus stopover requirements of young birds produced the following year, (2) local weather conditions interact with individual migrants' accumulated fuel stores to determine both the need to stopover (transience: largely fat-independent) and the duration of stopover (departure: highly fat-dependent), and (3) similar responses to environmental variability among diverse migrants using a common stopover may override species-specific stopover requirements and behaviour.

En route marking of individuals provides valuable information about migratory behaviour, and its relevance to the study of climatic influences extends to other migrants beyond passerine birds (e.g. Crozier & Zabel, 2006; Kéry et al., 2006). With enhanced awareness of the sensitivity of daily migration movements to environmental influences, we can better anticipate migratory shifts that may result from the continued climate change predicted by most models (e.g. Sillett et al., 2000; Lemoine & Bohning-Gaese, 2003; Bairlein & Huppop, 2004). Differences in climatic sensitivity among species, stopover sites, or regions could be used to prioritize those migrants expected to be most vulnerable to local or regional environmental change, and would be beneficial to the recognition and protection of critical stopover habitats (Mehlman et al., 2005). While known dangers to habitat and survival are incorporated in the designation and protection of endangered populations (e.g. Canada's Species at Risk Act), insight into climate-driven future threats to migrants' stopovers will be a valuable addition toward their conservation.

Acknowledgements

References

Adahl E, Lundberg P, Jonzén N (2006) From climate change to population change: the need to consider annual life cycles. *Global Change Biology*, **12**, 1627–1633.

Ahola M, Laaksonen T, Sippola K, Eeva T, Rainio K, Lehikoinen E (2004) Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology*, **10**, 1–8.

Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory* (eds Petrov BN, Csaki F), pp. 267–281. Akademiai Kiado, Budapest, Hungary.

Åkesson S, Hedenström A (2000) Wind selectivity of migratory flight departures in birds. *Behavioural Ecology and Sociobiology*, **47**, 140–144.

Åkesson S, Walinder G, Karlsson L, Ehnbom S (2001) Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. *Animal Behaviour*, **61**, 181–189.

Alerstam T (1979) Wind as a selective agent in bird migration. *Ornis Scandinavica*, **10**, 76–93.

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.

Alerstam T, Lindström A (1990) Optimal bird migration: the relative importance of time, energy and safety. In: *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner E), pp. 331–351. Springer-Verlag, Berlin.

Bairlein F (1990) Nutrition and food selection in migratory birds. In: *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner E), pp. 198–213. Springer-Verlag, Berlin.

Bairlein F, Huppop O (2004) Migratory fuelling and global climate change. *Advances in Ecological Research*, **35**, 33–47.

Bearhop S, Hilton GM, Votier SC, Waldron S (2004) Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society of London B*, **271**, S215–S218.

Brewer D, Diamond A, Woodsworth EJ, Collins BT, Dunn EH (2000) *Canadian Atlas of Bird Banding Volume 1: Doves, Cuckoos, and Hummingbirds through Passerines, 1921–1995*. Canadian Wildlife Service Special Publication, Ottawa.

Bruderer B, Liechti F (1998) Flight behaviour of nocturnally migrating birds in coastal areas - crossing or coasting. *Journal of Avian Biology*, **29**, 499–507.

Burnham KP, Anderson DR (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.

Cohen D (1967) Optimization of seasonal migratory behavior. *American Naturalist*, **101**, 5–17.

Crespin L, Harris MP, Lebreton J-D, Frederiksen M, Wanless S (2006) Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology*, **75**, 228–238.

Crozier L, Zabel RW (2006) Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. *Journal of Animal Ecology*, **75**, 1100–1109.

Danhardt J, Lindström A (2001) Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour*, **62**, 235–243.

Drent R, Both C, Green M, Madsen J, Piersma T (2003) Pay-offs and penalties of competing migratory schedules. *Oikos*, **103**, 274–292.

Dunn EH (2002) A cross-Canada comparison of mass change in birds during migration stopover. *Wilson Bulletin*, **114**, 368–379.

Dunn EH, Hobson KA, Wassenaar LI, Hussell DJT, Allen ML (2006) Identification of summer origins of songbirds migrating through southern Canada in autumn. *Avian Conservation and Ecology*, **1**, 4. [online] URL: http://www.ace-eco.org/vol1/iss2/art4/.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.

Fitzgerald T, Taylor P (2008) Migratory orientation of juvenile Yellow-rumped Warblers (*Dendroica coronata*) following stopover: sources of variation and the importance of geographic origins. *Behavioural Ecology and Sociobiology*, **62**, 1499–1508.

Forchhammer MC, Post E, Stenseth NC (2002) North Atlantic oscillation timing of long- and short-distance migration. *Journal of Animal Ecology*, **71**, 1002–1014.

Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S (2004) Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology*, **10**, 1214–1221.

Gauthreaux SA (1980) The influences of long-term and short-term climatic changes on the dispersal and migration of organisms. In: *Animal Migration, Orientation and Navigation* (ed. Gauthreaux SA), pp. 103–174. Academic Press, New York.

Gordo O, Sanz JJ (2006) Climate change and bird phenology: a long-term study in the Iberian Peninsula. *Global Change Biology*, **12**, 1993–2004.

Hallett TB, Coulson T, Pilkington JG, Clutton-Brock TH, Pemberton JM, Grenfell BT (2004) Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, **30**, 71–75.

Hedenström A, Alerstam T (1997) Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology*, **189**, 227–234.

Hunt PD, Eliason BC (1999) *Blackpoll warbler*. In: *The Birds of North America* (eds Poole A, Gill F), no. 431. Cornell Laboratory of Ornithology and The Academy of Natural Sciences, Ithaca, NY/Philadelphia, PA.

Huppop O, Huppop K (2003) North Atlantic oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London B*, **270**, 233–240.

Hurrell JW (1995) Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.

Hurrell JW, Kushnir Y, Ottersen G, Visbeck M (2003) An overview of the North Atlantic oscillation. In: *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*, pp. 1–35. Geophysical Monograph 134, American Geophysical Union, Washington, DC, USA.

Hussell DJT (1981) Migrations of the least flycatcher in southern Ontario. *Journal of Field Ornithology*, **52**, 97–111.

Intergovernmental Panel on Climate Change [IPCC] (2001) *Technical Summary of Working Group I*.

Jenni L, Kéry M (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London B*, **270**, 1467–1471.

Kaiser A (1993) A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology*, **64**, 246–255.

Kendall WL, Pollock KH, Brownie C (1995) A likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. *Biometrics*, **51**, 293–308.

Kéry M, Madsen J, Lebreton J-D (2006) Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology*, **75**, 1172–1181.

Klaassen M, Lindström A (1996) Departure fuel loads in time-minimizing migrating birds can be explained by the energy costs of being heavy. *Journal of Theoretical Biology*, **183**, 29–34.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Lehikoinen A, Kilpi M, Öst M (2006) Winter climate affects subsequent breeding success of common eiders. *Global Change Biology*, **12**, 1355–1365.

Lemoine N, Bohning-Gaese K (2003) Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology*, **17**, 577–586.

Lindström A, Alerstam T (1992) Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *American Naturalist*, **140**, 477–491.

Macmynowski DP, Root TL, Ballard G, Geupel GR (2007) Changes in spring arrival of Neoarctic–Neotropical migrants attributed to multiscalar climate. *Global Change Biology*, **13**, 2239–2251.

Marra PP, Francis CM, Mulvihill RS, Moore FR (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia*, **142**, 307–315.

Marra PP, Hobson KA, Holmes RT (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.

Martin GR (1990) The visual problems of nocturnal migration. *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner E), pp. 185–197. Springer-Verlag, Berlin.

Mazerolle DF, Dufour KW, Hobson KA, den Haan HE (2005) Effects of large-scale climatic fluctuations on survival and production of young in a Neotropical migrant songbird, the yellow warbler *Dendroica petechia*. *Journal of Avian Biology*, **36**, 155–163.

McWilliams SR, Guglielmo C, Pierce B, Klaassen M (2004) Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology*, **35**, 377–393.

Mehlman DW, Mabey SE, Ewert DN *et al.* (2005) Conserving stopover sites for forest-dwelling migratory landbirds. *Auk*, **122**, 1281–1290.

Møller AP (1994) Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioural Ecology and Sociobiology*, **35**, 115–122.

Morris SR, Holmes DW, Richmond ME (1996) A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor*, **98**, 395–409.

Nisbet ICT, McNair DB, Post W, Williams TC (1995) Transoceanic migration of the blackpoll warbler: summary of scientific evidence and response to criticisms by Murray. *Journal of Field Ornithology*, **66**, 612–622.

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM (2004) Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London B*, **271**, 59–64.

Peckford ML, Taylor PD (2008) Within night correlations between radar and ground counts of migrating songbirds. *Journal of Field Ornithology*, **79**, 207–214.

Prop J, Black JM, Shimmings P (2003) Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, **103**, 403–414.

Przybylo R, Sheldon BC, Merila J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *Journal of Animal Ecology*, **69**, 395–403.

Pyle P (1997) *Identification Guide to North American Birds: A Compendium of Information on Identifying, Ageing and Sexing "Near-Passerines" and Passerines in the Hand*. Slate Creek Press, California.

Pyle P, Nur N, Henderson RP, DeSante DF (1993) The effects of weather and lunar cycle on nocturnal migration of landbirds at Southeast Farallon Island, California. *Condor*, **95**, 343–361.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.

Ramenofsky M (1990) Fat storage and fat metabolism in relation to migration. *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner E), pp. 214–231. Springer-Verlag, Berlin.

Richardson WJ (1972) Autumn migration and weather in eastern Canada: a radar study. *American Birds*, **26**, 10–17.

Richardson WJ (1990) Timing of bird migration in relation to weather: updated review. *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner E), pp. 78–101. Springer-Verlag, Berlin.

Rivalan P, Frederiksen M, Loïs G, Julliard R (2007) Contrasting responses of migration strategies in two European thrushes to climate change. *Global Change Biology*, **13**, 275–287.

Rogers CM (1991) An evaluation of the method of estimating body fat in birds by quantifying visible subcutaneous fat. *Journal of Field Ornithology*, **62**, 349–356.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Sandvik H, Erikstad KE, Barrett RT, Yoccoz NG (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, **74**, 817–831.

Sanz JJ (2003) Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. *Ecography*, **26**, 45–50.

Schaub M, Jenni L (2001) Stopover durations of three warbler species along their autumn migration route. *Oecologia*, **128**, 217–227.

Schaub M, Liechti F, Jenni L (2004) Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour*, **67**, 229–237.

Schaub M, Pradel R, Jenni L, Lebreton J-D (2001) Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. *Ecology*, **82**, 852–859.

Sedinger JS, Ward DH, Schamber JL et al. (2006) Effects of El Niño on distribution and reproductive performance of black brant. *Ecology*, **87**, 151–159.

Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.

Stenseth NC, Mysterud A (2005) Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology*, **74**, 1195–1198.

Stenseth NC, Ottersen G, Hurrell JW et al. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic oscillation, El Nino Southern oscillation and beyond. *Proceedings of the Royal Society of London B*, **270**, 2087–2096.

Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. *Nature*, **406**, 366–367.

Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science*, **291**, 2598–2600.

Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–697.

Vahatalo AV, Rainio K, Lehikoinen A, Lehikoinen E (2004) Spring arrival of birds depends on the North Atlantic oscillation. *Journal of Avian Biology*, **35**, 210–216.

Visbeck MH, Hurrell JW, Polvani L, Cullen HM (2001) The North Atlantic oscillation: past, present and future. *Proceedings of the National Academy of Sciences of the USA*, **98**, 12876–12877.

Visser ME, Both C, Lambrechts MM (2004) Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research*, **35**, 89–110.

Weatherhead PJ (2005) Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. *Oecologia*, **144**, 168–175.

Weber TP, Alerstam T, Hedenström A (1998b) Stopover decisions under wind influence. *Journal of Avian Biology*, **29**, 552–560.

Weber TP, Ens BJ, Houston AI (1998a) Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology*, **12**, 377–401.

Weber TP, Fransson T, Houston AI (1999) Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds. *Behavioural Ecology and Sociobiology*, **46**, 280–286.

Weishampel JF, Bagley DA, Ehrhart LM (2004) Earlier nesting by loggerhead sea turtles following sea surface warming. *Global Change Biology*, **10**, 1424–1427.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, S120–S138.

White GC, Kendall WL, Barker RJ (2006) Multistate survival models and their extensions in Program MARK. *Journal of Wildlife Management*, **70**, 1521–1529.

Wiener P, Tuljapurkar S (1994) Migration in variable environments: exploring life-history evolution using structured population models. *Journal of Theoretical Biology*, **166**, 75–90.

Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH (2003) Avian metabolism: costs of migration in free-flying songbirds. *Nature*, **423**, 704.

Williams TC, Williams JM, Ireland LC, Teal JM (1977) Autumnal bird migration over the western North Atlantic Ocean. *American Birds*, **31**, 251–267.

Ydenberg RC, Butler RW, Lank DB, Guglielmo CG, Lemon M, Wolf N (2002) Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *Journal of Avian Biology*, **33**, 47–55.

Appendix A

Table A1 Species composition of the three groups of autumn migrants (early warblers, late warblers, sparrows) captured at Bon Portage Island, Nova Scotia, from 1996 to 2007, showing the total number of banded individuals used in the mark–recapture analyses

Abbreviations	Common name	Latin name	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	% of Total
Early warblers															
AMRE	American redstart	*Setophaga ruticilla*	115	17	49	49	28	140	46	42	59	36	67	39	24.1%
BAWW	Black-and-white warbler	*Mniotilta varia*	67	33	76	55	65	157	57	72	49	34	58	62	27.5%
COYE	Common yellowthroat	*Geothlypis trichas*	83	38	35	66	88	87	56	40	32	29	38	12	21.2%

Continued

Table A1 (Continued)

Abbreviations	Common name	Latin name	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	% of Total
Abbreviations	Common name	Latin name	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	% of Total
NOWA	Northern waterthrush	*Seiurus noveboracensis*	74	62	66	48	73	76	55	94	50	60	76	47	27.3%
		Total	**339**	**150**	**226**	**218**	**254**	**460**	**214**	**248**	**182**	**159**	**239**	**160**	**2849**
Late warblers															
MYWA	Yellow-rumped (myrtle) warbler	*Dendroica coronata coronata*	**222**	**220**	**172**	**579**	**507**	**346**	**369**	**134**	**NA**	**NA**	**187**	**210**	**2946**
Sparrows															
SCJU	Slate-coloured junco	*Junco hyemalis*	NA	57	27	17	18	64	14	18	NA	NA	NA	21	19.7%
SOSP	Song sparrow	*Melospiza melodia*	NA	82	49	24	59	57	30	30	NA	NA	NA	19	29.3%
SWSP	Swamp sparrow	*Melospiza Georgiana*	NA	71	33	8	40	15	12	10	NA	NA	NA	6	16.3%
WTSP	White-throated sparrow	*Zonotrichia albicollis*	NA	108	38	44	71	43	19	29	NA	NA	NA	63	34.7%
		Total	**NA**	**318**	**147**	**93**	**188**	**179**	**75**	**87**	**NA**	**NA**	**NA**	**109**	**1196**

NA: years in which the number of banded birds was too small to permit analysis. Note that the late warbler 'group' was restricted to only one species. Bold indicates the groups used in the analyses: Total early warblers, MYWA, Total sparrows.