

Effects of nutritional condition on spring migration: do migrants use resource availability to keep pace with a changing world?

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SUMMARY

Because of their reliance on temporally predictable resources across large spatial scales, migratory birds may be especially vulnerable to anthropogenic climate and land-use changes. Although some long-distance migrants appear unable to adjust to phenological shifts on their wintering grounds, several short- and medium-distance migrants appear to have altered the timing and/or distance of their yearly movements to compensate for the environmental effects of global warming. Which environmental cues are responsible for stimulating these adjustments is an unanswered question, although most studies have focused on weather conditions. Here, we present a novel field experiment that demonstrates that an alternative cue, food availability, may be a crucial link between local conditions on the wintering grounds and the timing of spring departure. When we provided dark-eyed juncos (*Junco hyemalis*) with an abundant food supply in early spring, we observed an advance in migration, especially among individuals that increased their mass and fat stores in response to the treatment. This finding indicates a simple mechanism by which short-distance migrants may calibrate their migration behavior such that arrival on the breeding grounds and initiation of reproduction are in sync with resource availability.

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Key words: timing of migration, nutritional condition, climate change, migratory fattening, food availability.

INTRODUCTION

Migratory animals must survive and reproduce using resources spaced across ecoregions and sometimes continents. Migrating birds, in particular, are heavily influenced by spatial and temporal variation in environmental conditions across their migratory route; therefore, these animals may be especially vulnerable to anthropogenic climate and land-use changes (Marra et al., 2005; Visser et al., 2004). Among long-distance migrants, several species appear unable to adjust to phenological shifts on their wintering grounds (Both and Visser, 2001), and some of their populations are suffering from the resulting temporal mismatch between resource availability and the demands of reproduction (Both et al., 2006; Visser et al., 1998). However, among short- and medium-distance migrants, several species appear to have altered the timing and/or distance of their yearly movements to compensate for the environmental effects of global warming (Gienapp et al., 2007; Gordo, 2007; Lehikoinen et al., 2004; Marra et al., 2005).

The timing of avian migration appears to be regulated by a combination of intrinsic and extrinsic cues. Among birds, there are species that will initiate migration at an appropriate time in the absence of any external stimuli (Berthold, 1984; Gwinner, 1996; Gwinner, 2000). Other species, usually short- or medium-distance migrants, may rely heavily on extrinsic factors such as daylength and weather conditions in determining exactly when to migrate (Berthold, 1975; Hahn et al., 2008). This reliance on extrinsic factors among short-distance migrants (as opposed to long-distance migrants) may be due to the increased likelihood that conditions on the wintering grounds are somewhat likely to reflect breeding-

ground conditions when these two habitats are relatively close together. In this study, we have examined the effect of a potentially important, but often overlooked, factor that might influence the seasonal movements of short-distance migrants: food availability.

Migration is an energetically expensive activity (Berthold, 1975; Wikelski et al., 2003). The accumulation of energy reserves prior to migration (i.e. migratory fattening) is a well-documented phenomenon in many migratory species (Bairlein, 2002). However, there is some uncertainty about what happens to migratory species when food supplies limit the degree of fattening they can achieve. Will migrants delay migration and suffer the consequences in terms of reproductive fitness (e.g. arriving too late to breed) and survival (e.g. negotiating the migration route during suboptimal conditions)? Or will the birds initiate migration and attempt to cope with the reduced fuel load, perhaps by stopping sooner than they otherwise would? Although the first strategy avoids the obvious dangers associated with depleting energy reserves, the second strategy may also be advantageous, as food-deprived birds may find more abundant resources at stopover locations, allowing them to recover their nutritional state and maintain a near-optimal migration schedule.

Most of what we know about the mechanisms underlying the timing of migration is based on observational data from wild birds (e.g. banding studies or correlations between weather data and bird abundance) or experiments on captive individuals (Gauthreaux, 1996; Gwinner, 2000; Jahn et al., 2004; Zehnder and Karlsson, 2001). Although they have yielded invaluable information, both of these approaches have important limitations. Observational studies

cannot ascertain causal relationships, as there may be variables at play beyond those that were monitored, and experiments on captive birds may not accurately reflect the real-world circumstances or behavior of wild birds. Our study is among the first to examine the timing of migration through the use of a field experiment. More specifically, we used a brief period of captivity to manipulate body mass and fat stores in a sample of otherwise free-living dark-eyed juncos (*Junco hyemalis*) wintering in central Oklahoma. We then released these individuals back onto their wintering grounds prior to spring migration and monitored them closely in order to determine when they left the area and presumably began their flight to the breeding grounds. Given the energetic expense of migratory flight (see Berthold, 1975; Wikelski et al., 2003) it stands to reason that spring departure can be constrained by body condition, such that birds without adequate energy reserves must delay migration until some threshold is reached. Our experiment tested a logical prediction from this hypothesis: that increasing body mass and fat reserves will encourage early migration, whereas a decrease in mass and fat will lead to delayed migration.

MATERIALS AND METHODS

Study system

Dark-eyed juncos were among the first species used to study the mechanisms underlying migratory behavior (see Rowan, 1925) and have been the subject of numerous other migration studies since then. Much of this work has focused on differences in migratory behavior in males and females, and has documented a general pattern in which males tend to migrate shorter distances and begin spring migration sooner than females (e.g. Chandler and Mulvihill, 1990; Ketterson and Nolan, 1976; Ketterson and Nolan, 1979; Yunick, 1988). Dark-eyed juncos are common throughout North America, with a broad breeding distribution across Canada and Alaska, and an equally expansive wintering population across most of the USA. The timing of migration varies regionally, but the birds generally leave the wintering grounds from early March to early April (Nolan et al., 2002).

Our study site consisted of ~16.5 ha of mown, open woodland that comprised the Aquatic Research Facility and some of the surrounding area near the southern tip of the University of Oklahoma Campus in Norman, Oklahoma, USA (35°10'58"N, 97°26'52"W). Juncos in this area appeared to consume primarily grass shoots until the emergence of dandelions and insects late in the study period. To our knowledge, they did not exploit birdfeeders or other anthropogenic food sources.

Bird capture and experimental treatments

Our study began during the winter of 2009 with a low-intensity mist netting effort on the study site, wherein five to 10 nets were deployed three or four times a week from 16 January to 25 February. For each bird captured, we recorded wing length, body mass and fat score. Fat scores were visually determined (Pyle, 1997) and ranged from 0 (no fat) to 5 (maximum fat). We also plucked the outermost secondary feather for stable isotope analyses and took a small (~10 µl) blood sample for genetic sexing. Each bird was banded with a numbered US Fish and Wildlife Service band on one leg and two color bands on the other leg. Each band combination was unique, allowing for visual identification of individuals in the field.

From 26 February to 2 March we carried out an intensive mist netting effort wherein we monitored 12 to 15 nets in various locations on the study site every day for 4–6 h. Birds captured during this period were processed as before (although many had been captured before and did not require banding or blood–feather

sampling), but were then held in captivity for a period of 5–7 days to allow us to carry out two captive feeding treatments. Birds were housed in individual cages within a large, insulated shed located at the Aquatic Research Facility. Lighting was provided by full-spectrum fluorescent bulbs and was timed to go on and off in accordance with local sunup and sundown. Captive birds were randomly assigned either to an *ad libitum* or to a food-restricted group. The 18 birds in the *ad libitum* group received a mixture of millet, sunflower hearts and mealworms, as well as a slice of orange and a piece of suet; this food mixture was refreshed daily such that all food types were always abundant during the captive period. This diet was derived from previous captive studies of dark-eyed juncos (e.g. McGlothlin et al., 2007; Thompson et al., 1987) with the intention of ensuring that the birds would gain mass during the captive period. Sixteen birds were assigned to the restricted diet and received 3 g of millet each day, with 2 g administered within 1 h of sunup, and 1 g delivered ~2 h before sundown.

Birds were maintained on their experimental diets for 5–7 days. Preliminary trials indicated that captive juncos generally lost weight during their first few days in a cage, and began to recover by day three (E.S.B. and J.F.K., unpublished). After 5 days of captivity, we weighed and scored fat for each bird. Birds on the restricted diet were then released if they had lost at least 1 g from their mass upon capture. Similarly, birds on the *ad libitum* diet were released if they added at least 0.5 g to their mass on capture. Otherwise the birds were kept in cages and fed their experimental diets for up to 7 days, after which birds were then released regardless of their mass. These procedures were reviewed and approved by the University of Oklahoma Institutional Animal Care and Use Committee prior to the study.

Resighting surveys

We conducted band-resighting surveys to determine when members of the different feeding treatments, as well as control birds (those banded but not held in captivity), left the study area. Beginning 3 March, surveys were generally conducted at least twice daily, and we inspected each of eight subdivisions (zones) within the study area at least once each day. Most sightings were recorded by making visual sweeps through ground-foraging flocks until we ceased to find any new individuals. Zones that appeared to be devoid of birds were quickly scanned and abandoned, such that we spent most of the time inspecting conspicuous flocks of juncos. Before releasing captive birds, we conducted several preliminary surveys both to confirm that resighting was possible and as a training exercise to ensure that our resighting abilities were consistent from the first post-release survey to the last. We excluded 1 day of survey effort (2 April) in which no birds were seen. The absence of juncos on this day was probably due to winds in excess of 50 km h⁻¹, which may have prevented normal foraging activities.

Genetic sexing

Although dark-eyed juncos are sexually dimorphic, males do not achieve adult plumage until the end of their first year. Consequently, it can be difficult to visually distinguish between first-year males and females of any age class (Nolan et al., 2002; Pyle, 1997). Hence, we genetically sexed most of the birds used in our study, including all birds that did not have definitive adult male plumage. Blood samples from birds in the field were temporarily stored in a TRIS-based lysis buffer and frozen after field work was complete each day. Genetic sexing was performed by ESB at the Molecular Ecology Laboratory within the University of Oklahoma Department of Zoology. DNA was isolated from blood samples using a Qiagen

DNeasy extraction kit (Valencia, CA, USA). We then carried out the PCR-based sexing protocol detailed by Griffiths et al. (Griffiths et al., 1998).

Hydrogen isotope analyses

Owing to latitudinal gradients in hydrogen isotope ratios in rainfall, the ratio of hydrogen isotopes in feathers indicates the latitude at which the feathers were grown. Migratory dark-eyed juncos molt their flight feathers on the breeding grounds (Nolan et al., 2002; Pyle, 2008); hence, hydrogen isotope ratios in the feathers we sampled should serve as an indicator of the migration distances of the birds we studied. Prior to stable-isotope analyses, all feathers were cleaned with dilute detergent and then a 2:1 chloroform–methanol solution (Paritte and Kelly, 2009). We then packed a 140–160 mg piece of the distal vane of each feather into a 3.5 mm × 5 mm silver capsule for insertion into an autosampling tray. Isotope ratio measurements were performed at the University of Oklahoma with a ThermoFinnigan Delta V isotope ratio mass spectrometer connected to a high-temperature pyrolysis elemental analyzer (TC/EA, Thermo-Finnigan, Bremen, Germany). Details for this particular analysis have been published previously (Kelly et al., 2009).

Data analysis

To determine whether there were differences in departure dates among the three treatment groups, we used the program MARK (White and Burnham, 1999) to implement the Cormack–Jolly–Seber (CJS) model for estimating survival from resighting data (Cormack, 1964; Jolly, 1965; Seber, 1965). This model incorporates information about when individuals were seen or not seen to estimate resighting probabilities (p_R), and these resighting probabilities are then used to estimate survival rates (ϕ), which we regarded as an indication of spring departure. Although death and departure are indistinguishable in this model, given the short time span (35 days) over which monitoring took place, we assume that the contribution of actual deaths to the estimates of ϕ were negligible. To evaluate the effects of our treatments, as well as sex and body condition, we constructed several models that systematically incorporated and excluded these variables, and we used Akaike's Information Criterion for small samples (AICc) to determine which models offered the most parsimonious explanation of our data.

Prior to model comparison, we used goodness-of-fit testing procedures implemented in MARK to ensure that our data agreed with the underlying assumptions of the CJS model. One hundred iterations of the bootstrapped goodness-of-fit test indicated that the observed deviance in our data did not exceed that of simulated data ($P=0.45$). Similarly the median c-hat test indicated an estimated c-hat of 1.17, which is similar to an ideal value of 1.

The first set of models began with a fully parameterized model incorporating treatment group and sex and a group–sex interaction term. We then simplified the model systematically such that all parameter combinations were implemented including a model with single estimates of ϕ and p_R . The resulting set of five models is fully described in Table 1.

To evaluate responses to the feeding treatments, we developed a body condition index that incorporated both mass and fat score. Deriving this index was complicated by the fact that mass is inherently related to linear body size (larger birds are heavier), whereas fat score is independent of size. Hence, we used the residuals from a regression of mass on wing cord to derive a mass value that was uninfluenced by overall size (Green, 2001) (see supplementary material Fig. S1). We then calculated the first principal component of this mass value and fat score, and multiplied it by -1 to generate a condition index in which larger values corresponded to heavier, fatter birds.

For each bird subjected to a feeding treatment (both *ad libitum* and restricted), we calculated the body condition index twice: once using data collected upon capture and again using data taken immediately prior to release. Although similar data were collected for control birds, these measures often were made several weeks before resighting surveys began. Because of the potential for mass and fat score to change over the course of the season, it would be inappropriate to compare mass and fat data among captive and control birds. Hence, we evaluated the potential for mass and fat score to influence the initiation of spring migration on a reduced dataset that included only the temporarily captive birds. Using this subset of data, we evaluated a new set of models in MARK, wherein the release condition index described above could be incorporated as an individual covariate. Our choice of modeling parameters was similar to that of our previous effort in that we used p_R and ϕ parameters that were constant over time. Hence, the models varied in their inclusion of treatment group, sex and the condition index. For simplicity, the model set presented here includes only main effects. We explored the influence of two-way interactions on model fit, but these models did not enhance the interpretation of the data and are not discussed in detail. In total we evaluated eight models for this second data set, all of which are listed in Table 2.

We note that this analytical approach precludes the notion of traditional statistical testing based on P -values (Burnham and Anderson, 2002). Instead, inferences from the data are made based on strength of evidence (Royall, 1997). Nevertheless, in order to aid the interpretation of our results, we performed some simple statistical tests to examine how the feeding treatments related to when the birds were last seen during our resighting surveys. These last-seen dates may not accurately reflect when a bird actually began its spring migration, but, given that the daily resighting probability

Table 1. Models with associated output parameters for evaluating the effect of sex and treatment group on apparent survival (ϕ)

Model	AICc	Δ AICc	AICc weight	K	Deviance	Parameter estimate (β) \pm s.e.m.	
						Sex	Grp
$\phi(\text{sex} + \text{grp})$	1547.41	0	0.41	4	1539.35	-0.81 ± 0.30	0.25 ± 0.17
$\phi(\text{sex})$	1547.51	0.1	0.39	3	1541.48	-0.81 ± 0.30	–
$\phi(\text{sex} + \text{grp} + \text{sex} \times \text{grp})$	1549.35	1.94	0.16	5	1539.26	-1.04 ± 0.82	0.18 ± 0.29
$\phi(\text{grp})$	1553.47	6.07	0.02	3	1547.44	–	0.24 ± 0.17
$\phi(.)$	1553.49	6.08	0.02	2	1549.47	–	–

The acronyms 'grp' and 'sex' indicate that separate ϕ values were estimated for the different treatment groups and for males and females, respectively. 'sex × grp' indicates an interaction term and $\phi(.)$ indicates model with a single ϕ estimate for all birds. The K column shows the number of parameters in each model. All models also included a single resighting probability parameter; hence, the $\phi(.)$ model has two parameters.

Table 2. Models with associated output parameters for evaluating the effects of sex, treatment group (Grp) and condition (Cond) on apparent survival (ϕ)

Model	AICc	Δ AICc	AICc weight	K	Deviance	Parameter estimate (β) \pm s.e.m.		
						Sex	Cond	Grp
$\phi(\text{sex} + \text{cond})$	783.5	0	0.58	4	775.38	-0.97 ± 0.40	-0.52 ± 0.16	–
$\phi(\text{sex} + \text{cond} + \text{grp})$	784.93	1.43	0.28	5	774.74	-0.98 ± 0.40	-0.65 ± 0.24	0.44 ± 0.55
$\phi(\text{cond})$	787.74	4.24	0.07	3	781.67	–	-0.47 ± 0.17	–
$\phi(\text{cond} + \text{grp})$	789.36	5.86	0.03	4	781.24	–	-0.59 ± 0.24	0.35 ± 0.54
$\phi(\text{sex} + \text{grp})$	790.29	6.8	0.02	4	782.17	-0.83 ± 0.39	–	-0.60 ± 0.38
$\phi(\text{sex})$	790.78	7.28	0.02	3	784.71	-0.80 ± 0.38	–	–
$\phi(\text{grp})$	793.05	9.55	0.01	3	786.97	–	–	-0.55 ± 0.37
$\phi(.)$	793.25	9.75	0	2	789.21	–	–	–

Symbol notation is the same as in Table 1, except for the addition of condition (Cond). The treatments groups in these models consist of only the *ad libitum* and food-restricted groups, as the control group lacked a comparable release-condition variable.

was ~ 0.6 (according to our modeling in MARK), last-seen dates should be a useful index of departure date. Analyses other than those performed in MARK were carried out in R (R Development Core Team, 2004). Means and parameter estimates presented below are accompanied by standard deviations (s.d.) or 95% confidence intervals (c.i.).

RESULTS

Stable isotope analyses

Hydrogen isotope ratios from 80 juncos captured at our study site, including all but four birds used in the feeding experiment, averaged $-148.8 \pm 13.8\%$ (s.d.) and ranged from -118.6 to -175.6% (parts per thousand deviation from Standard Mean Ocean Water). The distribution of the data approximated normality, with no indication of bimodality or pronounced skew (see supplementary material Fig. S2), which might indicate representatives from multiple breeding populations. Inference of molting locations from stable isotopes is limited with respect to individual birds (Kelly et al., 2002; Wunder and Norris, 2008); however, by comparison with isotope ratios in precipitation (Bowen and Revenaugh, 2003) (or waterisotopes.org), we can safely assume that all of the birds captured molted north of 46°N latitude, and may have ranged into Canada's Northwest Territory.

Effects of feeding treatments on mass and fat

Birds subjected to the food-restricted diet lost an average of 2.25 ± 0.43 g (c.i.) – about 11% of their original body mass – during the captive period, and half of them showed a decrease in fat score. Among the 18 birds on the *ad libitum* diet, twelve gained mass, three birds did not alter their mass and three others lost mass (< 1 g in all cases). The average change in mass for *ad libitum* birds was a gain of 0.84 ± 0.44 g (c.i.; Fig. 1). Fat scores generally increased among the *ad libitum* birds, and there were no decreases in fat score in this group. Upon release, 13 of the *ad libitum* birds had very high fat scores (four or five; Fig. 1).

Resighting surveys

As a preliminary evaluation of our resighting data we compared total survey duration for each day to the number of birds resighted that day over the first 26 survey days (the days in which there were at least 10 birds known to be present). Although survey times varied from 78 min to 236 min, the ratio of banded birds sighted to the total number known to be present (based on subsequent resightings) remained fairly constant at 0.64 ± 0.12 (mean \pm s.d.), and a simple regression of resighting percentage versus survey time was

insignificant ($R^2=0.05$, $P=0.79$). We believe that during each day of survey effort, the proportion of birds resighted increased rapidly before quickly leveling off with increasing survey time. Furthermore, the vast majority of our surveys were, we believe, sufficiently long to allow the number of resighted birds to approach the asymptote. Our initial modeling efforts in MARK using the comprehensive data set indicate a robust effect of sex but a relatively weak effect of treatment group. The most parsimonious model included both treatment group and sex, but this model was only slightly better than the model that incorporated sex only (Δ AICc=0.1). The three models that incorporated sex accounted for 99% of the AICc weight, and the parameter estimate (β) for sex in the best model was -0.80 ± 0.59 (c.i.), which clearly indicates the importance of sex in relation to apparent survival. Although treatment group was a factor in the best model, its parameter estimate, 0.25 ± 0.31 (c.i.), was less robust than that of sex (Table 1).

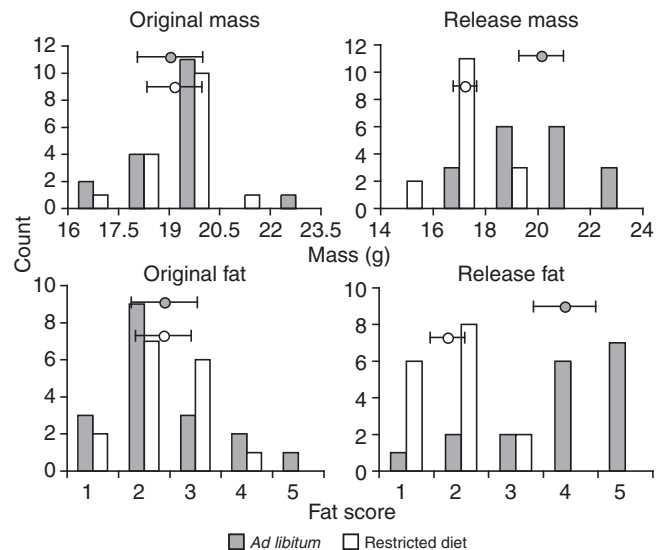


Fig. 1. Histograms showing how feeding treatments affected mass and fat score. Histograms in the left column show conditions observed prior to feeding treatments, and histograms on the right illustrate the same parameters immediately before birds were released. Dots and error bars denote means and 95% confidence intervals for the two treatment groups. The scales of the x-axis for the top left and top right histograms differ slightly.

The second set of models for which we evaluated the effect of release condition on ϕ in the temporarily caged birds, provided a much clearer indication of an effect on the timing of spring migration. As with the previous analysis, sex was an important parameter in the model set ($\beta \pm \text{s.e.} = -0.97 \pm 0.78$ in the best model), and it appeared in the two most parsimonious models, which accounted for about 86% of the AICc weight of the model set. However, the release condition co-variate was also influential ($\beta \pm \text{s.e.} = -0.61 \pm 0.31$ in the best model) as every model that incorporated this parameter outranked the models that did not. Not surprisingly, the most parsimonious model included both sex and release condition (Table 2). Treatment group was not in the best model and appeared to have limited influence in models with condition as a co-variate (see Table 2), which indicates a relationship between treatment group and condition and a stronger effect of condition. Models that incorporated interaction terms (not presented here) also indicated the importance of sex and condition, but were generally inferior to main-effects models with similar parameters.

Our examination of last-seen dates mirrored the results of the mark-recapture analysis. There was a clear difference in last-seen dates between the sexes, with females leaving later than males ($F_{1,55} = 27.0$, $P < 0.001$; Fig. 2). Last-seen dates (day of year) for the *ad libitum* group averaged 74.4 ± 10.1 (s.d.), which was slightly lower than the means for the restricted group [81.0 ± 8.4 (s.d.)] and the control group [80.2 ± 7.8 (s.d.); $F_{2,55} = 3.1$, $P = 0.053$]. When we examined last-seen dates in relation to individual responses to the feeding treatments, we saw a significant effect of sex ($F_{1,30} = 10.5$, $P < 0.001$) and a negative relationship with release condition (birds in better condition left sooner; $F_{1,30} = 10.1$, $P < 0.001$; Fig. 2).

DISCUSSION

An unambiguous effect of treatment group on apparent survival (i.e. spring departure) was absent in our results. However, it was clear that birds in the *ad libitum* group that substantially increased their body mass and fat reserves in response to an unlimited food supply became absent from the resighting surveys (i.e. departed) sooner than most of the other temporarily captive birds, as well as the unmanipulated controls (see Figs 1 and 2). We explain the lack of a straightforward treatment effect as a result of the substantial individual variation in responses to captive feeding in the *ad libitum* feeding group (Fig. 2). Our results indicate that the ability to store fat mediated through food availability may be an important determinant of when juncos migrate. In situations where wintering and breeding habitats are close enough that they both are affected by the same large-scale climatic or biotic phenomena, this effect of food availability on the timing of migration may serve as a mechanism that helps birds fine tune their spring migration to synchronize their breeding cycle with resource availability in the breeding habitat.

Rogers (Rogers, 1995) has demonstrated that fat storage in wintering dark-eyed juncos is a particularly plastic trait that can increase rapidly in response to decreases in temperature. Rogers (Rogers, 1995) did not attempt to establish a direct link between fat storage and food availability; rather anticipation of food shortages in association with cold conditions was seen as an ultimate cause of fat deposition (Rogers et al., 1994). Among the few studies that do examine diet in relation to the timing of migration, the results are mixed. Observational studies tend to show that early migration is associated with good body condition (Bauer, 2006; Marra et al., 1998), and studies at migratory stopover locations indicate that birds with abundant fat stores delay migration less than those with little fat (Cherry, 1982; Schaub et al., 2008). Conversely, captive hermit

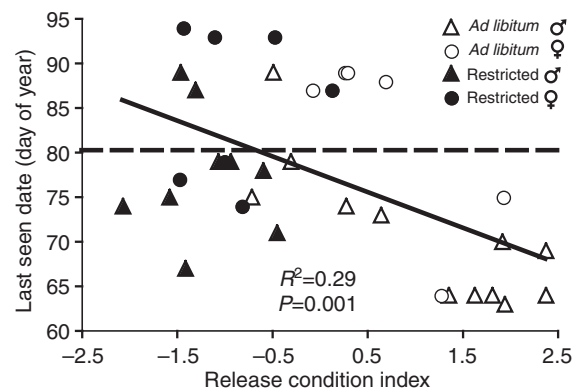


Fig. 2. Last-seen dates versus release condition for birds subjected to the feeding treatments. The solid line is the result of a linear regression with members of both feeding groups and sexes pooled. The broken line corresponds to the mean last-seen date for the control birds (i.e. those not subjected to a captive feeding treatment).

thrushes (*Catharus guttatus*) fed experimental diets indicated no effect of food on the timing of migratory restlessness (Long and Stouffer, 2003). However, each of these studies is based on either observational data or captive populations and is subject to the shortcomings discussed earlier.

Although migratory fattening is a well-documented phenomenon in many bird species (Bairlein, 2002), the physiological link between fat deposition and migratory behavior has not been fully explored. It is possible that glucocorticoid stress hormones may play a role in the signaling pathways that mediate migration (Holberton and Able, 2000). Given that elevated corticosterone is often associated with food limitation (Jenni-Eiermann et al., 2008; Kitaysky et al., 1999; Schoech et al., 2004), this hormone may have the potential to regulate migration in accordance with nutritional state.

Numerous biomechanical models of avian migration regard nutritional condition or 'fuel load' as a vital parameter in determining the duration and range of migratory flight (Hedenström, 1992; Hedenström, 2008; Lindström and Alerstam, 1992), yet most studies of the timing of migration tend to focus primarily on the roles of photoperiod and weather variables (Berthold and Terrill, 1991; Gauthreaux, 1996). This inattention to the direct effect of food is puzzling. Perhaps it is assumed that there are no meaningful restrictions on food intake during early spring, such that birds are free to initiate migratory fattening at any time. Although an overabundant food source may be a reality for captive birds, it is an unlikely prospect for free-living individuals. We note that the birds in our experiment that substantially increased their fat reserves not only left earlier than the birds on the restricted diet, but also departed before birds in the control group. This result could be indicative of restricted food intake in the control group that prevented early spring migration, which would mean that food limitations on the wintering grounds do occur in early spring.

Appropriate timing of spring migration is vital to ensuring a balance between resource availability and the demands of reproduction, and the rapid climatic changes predicted for temperate regions in the coming decades (Meehl et al., 2005) may make this balance more and more elusive. Migratory birds will undoubtedly be affected by changes in our climate, but they may also be capable of responding to these changes in their environment by altering their migration schedule (Marra et al., 2005). Clearly, a better understanding of the mechanisms by which some species –

particularly short-distance migrants – adjust the timing of spring migration would both improve our ability to forecast how birds will respond to global warming and inform conservation decisions.

LIST OF ABBREVIATIONS

AICc	Akaike's Information Criterion for small samples.
c.i.	95% confidence interval
CJS	Cormack–Jolly–Seiber mark–recapture model
p_R	resighting probability
s.d.	standard deviation
β	model parameter effect size
ϕ	apparent survival rate

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