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Title: Social environment influences termination of nomadic migration

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Running header: Social environment and termination of migration

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Abstract

The final stage of migration, when animals terminate migratory movements and transition to a more sedentary state, remains the least understood phase of migration. Whereas migrants that return to the same locations each year may use mechanisms associated with locating a specific destination, migrants with low site fidelity, such as nomadic migrants, may rely on local environmental cues to determine when to cease migratory movements. Using an experiment with captive birds, we tested whether the presence of a conspecific influences the termination of migration, indicated by changes in behaviour and physiology, in a nomadic migrant (the pine siskin, *Spinus pinus*). We paired migratory birds with a non-migratory individual or left migratory and non-migratory individuals unpaired. Migratory paired birds had a significant decline in nocturnal activity immediately after pairing and activity levels remained lower two weeks later, with significant declines in energetic reserves and flight muscle size also observed. In contrast, migratory unpaired birds maintained high levels of activity and energetic reserves. These results provide evidence for a role of the social environment in migratory termination decisions. Social cues may be particularly useful in nomadic migrants, such as pine siskins, to facilitate settling in high quality, but unfamiliar, habitats.

Keywords: facultative migration, nomad, settlement, social, termination

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1. Introduction

Social interactions are known to be important in migratory decision-making, influencing directional and navigational decisions [1-4]. However, relatively little is known about the role of social cues in migratory departure, stopover, and termination decisions, though a few studies point to their potential importance [5-11].

The settlement, or termination, phase of migration, when animals transition from persistent movement to a more sedentary state, is arguably the least understood phase [12, 13], but has important consequences for fitness [14, 15]. For migrants with a specific destination, such as to-and-fro migrants that return to the same wintering and breeding grounds, arrival at a recognized site and/or a specific internal program of migratory distance and direction could serve to trigger migratory termination [16-19]. However, many other animals have low site fidelity, migrate without a specific destination [12], and cannot make use of such mechanisms; these species instead may use local environmental cues, such as temperature, food availability, habitat features or cues from others, to make settlement decisions. Yet few studies have empirically tested the role of such local cues.

Nomadic migrants, whose movements are highly variable in direction, route, and destination from year to year, are likely to rely heavily on local cues to make settlement decisions [20, 21]. Nomadic migrations typically facilitate the use of resources that are rich, but ephemeral, and occur relatively unpredictably in space and/or time [21-23]. A classic example of such nomadic migrants are birds that feed on conifer seeds, which can vary dramatically in abundance at a given location from year to year and between locations within a given year [22, 24, 25]. Assessment of patch quality and foraging conditions is likely critical to the migratory decisions of these nomads [23, 26], with cues from conspecifics providing a potentially important source of information for these assessments [21, 27-29].

We used captive pine siskins (*Spinus pinus*) to test the hypothesis that the social environment influences the decision to terminate migration in a nomadic migrant. Although pine siskins are highly flexible in the timing of migrations, they exhibit a relatively predictable period of spring nomadism [30]. In captivity, spring nomadism is characterized by physiological preparations, including fat deposition and flight muscle hypertrophy, followed by the expression of nocturnal migratory restlessness [31]. During this period of spring nomadism, we tested whether the presence of a conspecific stimulated changes in behaviour and physiology indicative of termination of migration. Migratory birds were either paired with a non-migratory conspecific or left unpaired as a control, with an additional control group of non-migratory birds that also remained unpaired. We predicted that if pine siskins use the presence of a conspecific as a cue to terminate migratory movements, then paired migratory birds would reduce migratory restlessness and alter physiological traits that support migration (e.g., reduce fat deposits and body mass), while migratory birds that remained unpaired would maintain migratory restlessness and physiology.

2. Material and Methods

A detailed description of the methods is provided in the electronic supplementary material.

(a) Experiment

Pine siskins (n = 44) were captured at sites across the western United States and transported to Loyola Marymount University, Los Angeles, CA, USA. Birds were housed indoors on a photoperiod that mimicked naturally changing day length (42°N latitude) and provided ad libitum water, grit, pelleted maintenance diet, and a seed mixture. All subjects were male to control for possible influences of intersexual interactions. We placed birds in individual cages prior to the start of the experiment; birds had auditory, but not visual, access to all experimental birds throughout the experiment.

This experiment occurred in the late spring when pine siskins typically terminate expression of migratory restlessness. Birds were initially categorized as migratory or non-migratory, and then assigned to be either unpaired (control) or paired to generate 4 treatment groups. Birds in the migratory and non-migratory control groups (n = 11 birds each) remained unpaired for the duration of the experiment, whereas paired birds were subsequently housed with another male of the opposite migratory status (n = 11 pairs; one migratory and one non-migratory bird in each pair). This experimental design does not allow assessment of whether birds are responding to the migratory state of a conspecific or merely the presence of a conspecific. But pairing birds of opposite migratory status was expected to elicit a strong response if birds are sensitive to social environment. Because of logistical constraints, birds were run through the experiment in 5 groupings (with 5-11 birds per group) between 14 May – 11 June 2017.

Prior to the experimental manipulation, initial data were collected ("Pre" phase, Days 1-2; Figure 1), including video recording birds on two consecutive nights. To determine initial migratory/non-migratory state of birds, one observer (ARR) viewed the videos on the morning of Day 3 and categorized birds as either migratory or non-migratory based on overall nocturnal activity levels (these assignments were later confirmed as described below). Once migratory status was determined, birds were randomly assigned to be either unpaired or paired in as balanced a manner as possible within and across groupings (see electronic supplementary materials).

On Day 3, following assignment to treatment groups, we made body measurements, then paired birds by placing a non-migratory bird in the cage of its assigned migratory partner, and monitored pairs for excessive aggression. Four pairs exhibited high levels of aggression, and we removed one bird and replaced it with a bird of the same migratory status from the same grouping (see electronic supplementary materials). No further aggression was observed after these pairs were finalized. We video recorded birds for two consecutive nights starting on the evening of Day 3 ("Initial" phase) and again for two consecutive nights between 9 and 11 days later ("Final" phase). Final body measurements were made after completion of all video recordings. This was done 0 to 2 days after the final recording for all birds except for those from one grouping (n = 9) that were remeasured 12 days after their final recording (see electronic supplementary material for analysis indicating that this difference did not influence results).

(b) Behavioural and body measurements

We scored behaviour between 23:00 – 3:00, when pine siskins typically exhibit nocturnal migratory restlessness [32], using instantaneous scan sampling [33] at 5-min intervals. One of two observers (HXZ, WN) scored each video and recorded the behaviour at each interval as: stationary, jumping, flight, fast wing beating, beak up hopping, feeding, preening, or "other" (electronic supplementary materials, Table S3). We included aggressive behaviours in the list of behaviours to be scored, but they were not observed. We summed the frequency of jumping, flight, fast wing beating, and beak up hopping to calculate the proportion of time that each bird engaged in locomotor behaviour as a measure of nocturnal migratory activity. Behavioural data were averaged across the two recordings from each phase (Pre, Initial, and Final) to calculate the mean proportion of locomotor activity (hereafter "activity"). Observers were blind as to whether birds had been initially categorized as migratory or non-migratory and had high inter-observer reliability (intraclass correlation coefficient = 0.975, 95% CI [0.885, 0.995].

Birds were weighed to the nearest 0.01 g to measure body mass. Furcular and abdominal fat deposits were scored on a scale from 0 to 5 [34] and summed to estimate fat deposits. Flight muscle size was scored visually on a scale from 0 to 3 [35].

(c) Statistical analysis

We used JMP Pro 14.0 (SAS Institute Inc., Cary, NC, USA) and R v.3.5.2 [36] for analyses. Activity data were log transformed to meet model assumptions. Principal components analysis was used to distill mass and summed fat score into a single variable; the principal component (hereafter, "body condition") loaded positively for both mass and fat (0.96 and 0.96, respectively; eigenvalue = 1.84) and explained 91.86% of the variance. To confirm initial assignment of birds to migratory and non-migratory states, we compared groups during the Pre phase using ANOVAs for activity and body condition and a Kruskal-Wallis test for muscle size. To evaluate the effect of pairing on activity and body condition, we used linear mixed models with treatment, experimental phase, and their interaction as fixed effects. Model effects were tested using Satterthwaite's method (lmerTest package [37]) and semi-partial R^2 values were calculated for effects (r2glmm package [38]). We used cumulative link mixed models and likelihood-ratio tests to analyze the effect of treatment, experimental phase, and their interaction on muscle size (ordinal package [39]). All mixed models included bird ID nested within grouping to account for the different start dates as random effects (random intercepts). We tested for differences between phases of the experiment within treatment groups using Tukey's HSD test in the emmeans package [40].

3. Results

Behavioural and body condition data from the Pre phase confirmed initial assignments of birds to migratory/non-migratory states (electronic supplementary material, Figure S2); migratory birds had significantly higher activity levels ($F_{3,\,40} = 8.83$, $p < 0.001$) and body condition ($F_{3,\,40} = 8.42$, $p = 0.0002$) compared to non-migratory birds, though muscle size did not differ ($\chi^2_3 = 3.04$, $p = 0.39$). We also confirmed that within migratory/non-migratory state, activity and body condition did not differ at the Pre phase between birds assigned to be paired or unpaired (Figure S2). Changes in nocturnal activity across the experiment differed significantly among treatment groups (Table 1). Migratory paired birds, but not migratory unpaired controls, had significantly lower activity levels during the Initial and Final phases compared to their Pre activity, while non-migratory paired birds had significantly higher activity at the Final phase compared to their Pre levels (Figure 2a; Table S4). Changes in body condition over the experiment also differed among treatment groups (Table 1). Only migratory paired birds had significantly lower body condition at the Final phase compared to the Pre phase (Figure 2b). Muscle size declined significantly during the experiment (Table 1); pairwise comparisons within treatment groups indicated a significant decline in size only in the migratory paired birds (Figure 2c).

4. Discussion

This study reveals that the social environment can rapidly alter migratory behaviour and physiology in pine siskins, potentially facilitating the termination of migration and settlement. When paired with a non-migratory conspecific, migratory birds reduced their nocturnal activity and their energetic reserves and flight muscle size, which are physiological traits that support migration. These changes parallel those seen in other migrants during migratory termination [41] and contrast with the lack of changes in nocturnal activity or physiology among migratory birds that remained unpaired in our experiment. The difference in response between the two migratory groups suggests that auditory cues alone are not sufficient to induce settlement as all birds had auditory access to both migratory and non-migratory birds within the room. Although it is possible that changes in behaviour and physiology of migratory paired birds were due to competition with and/or aggression from their non-migratory cagemates, we believe this explanation is unlikely. First, aggression was not observed after pairings were finalized. Second, for competition or aggression to explain our results, non-migratory birds would need to be consistently dominant/aggressive to migratory birds; however, there was no clear pattern that migratory status influenced a bird's initial behaviour towards its cagemate (see electronic supplementary material). Lastly, birds had an excess of food provided in more than one cup, and both birds within the cage were observed feeding in videos, suggesting that declines in body condition in migratory paired birds was not due to exclusion from food. We cannot determine if the migratory paired birds altered their behaviour and physiology in response to the presence of a conspecific or were responding more specifically to the migratory status of the conspecific. It is plausible that pine siskins might use either presence/absence information or information about the state of conspecifics during decision-making about when and where to terminate migration; further work will be needed to distinguish between these alternatives. Given that the exact timing and location of suitable conditions for breeding occur relatively unpredictably across years for this species, the presence of settled conspecifics may be a particularly good indicator of potentially high-quality breeding habitat. Although the extent to which other species are similarly sensitive to the social environment during migratory termination remains to be determined, social cues may be important in numerous species, particularly other nomadic migrants [42, 43].

Unexpectedly, the non-migratory paired birds showed a significant increase in nocturnal activity during the Final phase (9-11 days after pairing) compared to Pre levels. Because their migratory partners maintained low levels of nocturnal activity, the increase in activity of the non-migratory partners could reflect behavioural synchronization of pairs. Social synchronization of daily activity patterns is known to occur in many species [44, 45], and could be important in flocks of pine siskins. Maintenance or resumption of low activity levels could also reflect a two-phase settlement process in which migratory termination begins with the cessation of large-scale movements, but local movements or a readiness to move can persist until settlement is complete [46, 47]. Thus, the low activity level observed in paired birds could reflect readiness, and possibly synchronization, for local movements.

Social cues are known to play an important role in habitat selection, including in the context of migration and breeding [48]. For instance, birds use conspecific and heterospecific cues in habitat selection during migratory stopovers [8, 9] and to select breeding sites [10, 11, 49-51]. Although many of the studies of breeding site selection have been conducted in migratory species, neither these nor the stopover studies were designed to distinguish whether social cues/environment influenced the cessation of migration per se or instead habitat selection once the process of settlement or stopover had already begun. Thus, we believe this is the first study to provide experimental evidence that the social environment can influence migratory behavior and physiology associated with the termination of migration.

Ethics

Birds were collected under scientific permits from the U.S. Fish and Wildlife Service and the states of California, Oregon, Washington, and Wyoming. All procedures were approved by the Loyola Marymount University Institutional Animal Use and Care Committee (protocol: LMU IACUC 2014 FA 02).

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Table 1. Linear mixed model results for model effects.

Response variable	Treatment			Phase			Treatment x Phase		
	F_{df}	p	R^2*	F_{df}	p	R^2*	F_{df}	p	R^2*
Activity	$16.84_{3,37.91}$	<0.0001	0.57	$7.45_{2, 80}$	0.001	0.16	$9.65_{6, 80}$	<0.0001	0.42
Body condition	$4.22_{3,40.14}$	0.01	0.24	$2.45_{1,39.48}$	0.13	0.06	$4.76_{3,39.46}$	0.006	0.27
	χ^2_{df}	p		χ^2_{df}	p		χ^2_{df}	p	
Muscle size	2.14_3	0.54		11.19_1	0.0008		2.97_3	0.40	

*Semi-partial R^2 values

Figure 1. Timeline showing collection of nocturnal behavioural data (video) and body measurements across phases of the experiment.

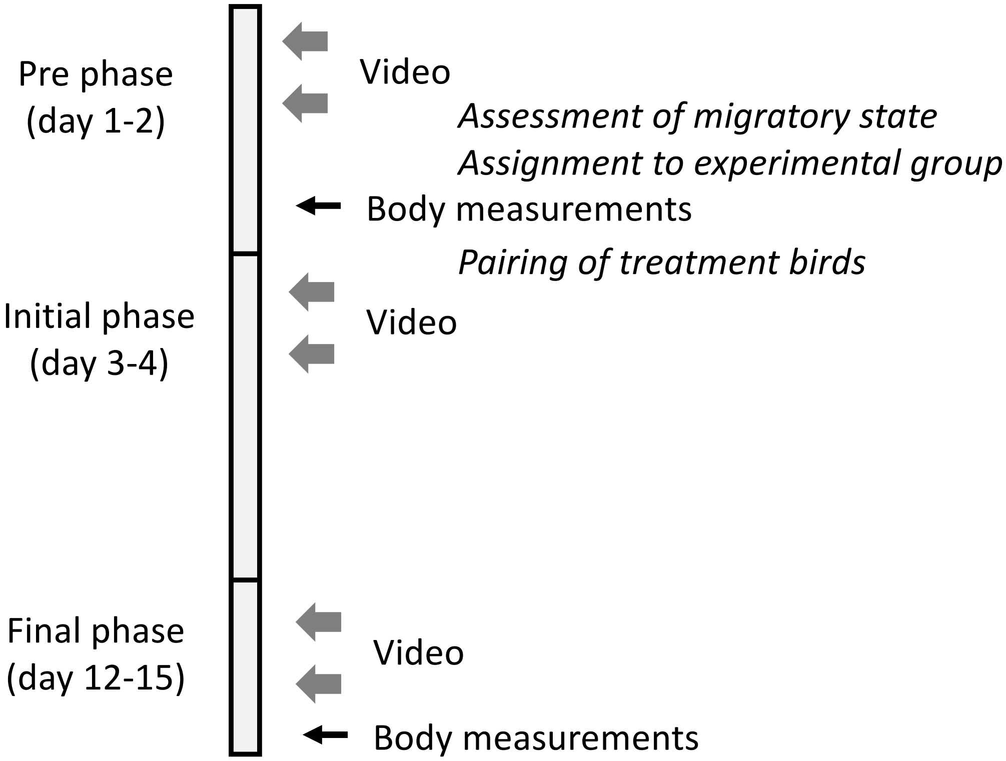

Figure 2. Nocturnal activity (a), body condition (b), and flight muscle size (c) during the Pre (dark grey), Initial (light grey), and Final (white) phases of the experiment for migratory and non-migratory birds that were either paired with a bird of the opposite migratory status after the Pre phase or remained unpaired. Higher values for body condition indicate greater mass and fat. Asterisks denote significant changes (* = $p < 0.05$, *** = $p < 0.0001$) between phases within a treatment group indicated by Tukey HSD. Bars represent mean ± 1 standard error; n = 11 for all treatment groups at all phases, except n = 10 for body condition and muscle size for the non-migratory paired group during the Final phase.

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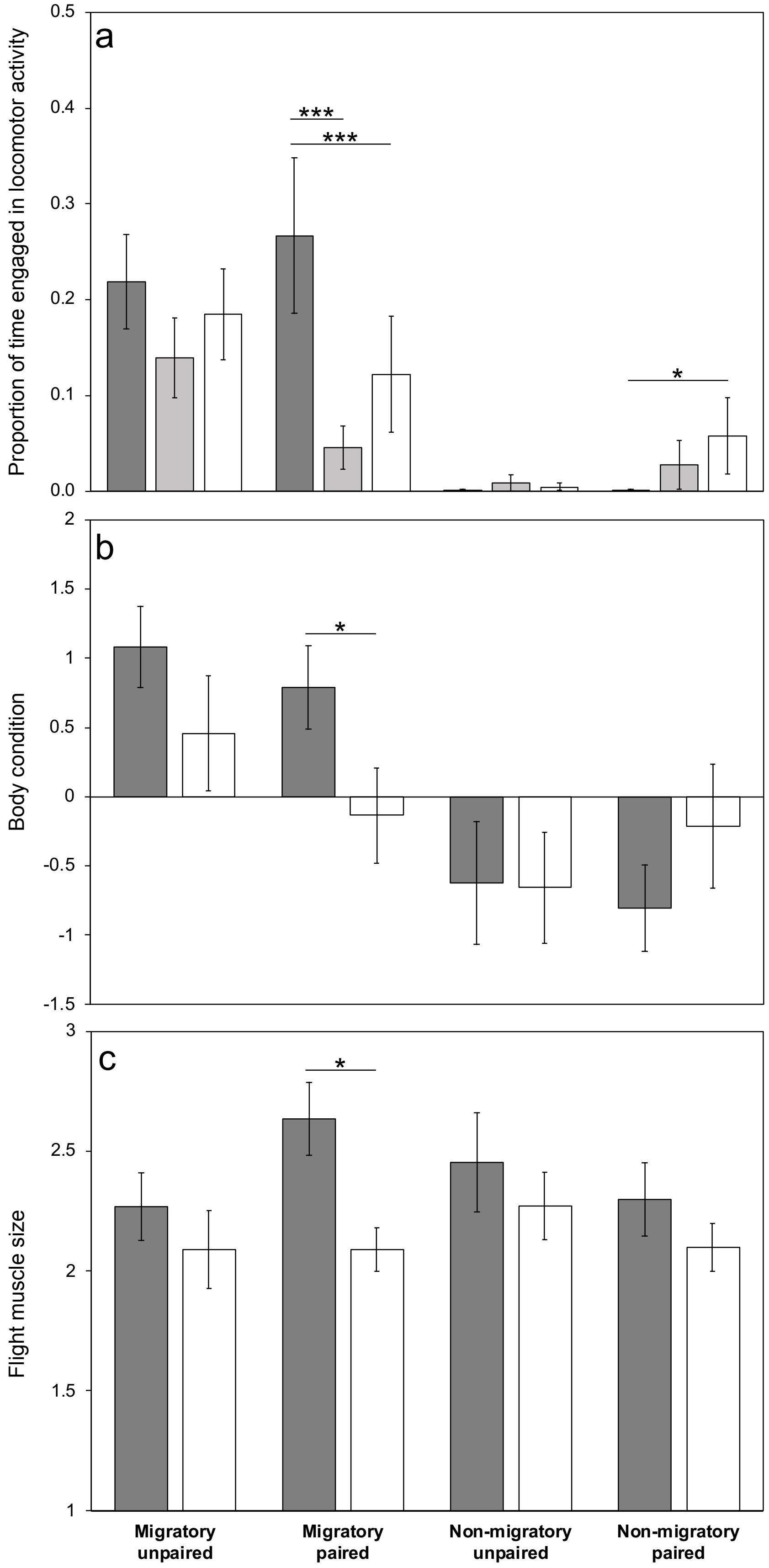

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