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TITLE Social information use in migratory decision-making depends upon conspecific state

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ABSTRACT

Social information is widely used by animals to inform decisions made in a variety of contexts. Less well understood is how the state of the information source influences social information use and if social information informs migratory decisions. Further, most studies on social information use in the context of migration focus on obligate migrants, yet social information is predicted to be particularly important for species that exhibit more flexible migratory behavior. We experimentally tested for social cue use during the vernal migratory period in a captive population of pine siskins (*Spinus pinus*). Pine siskins are nomadic migrants that exhibit a highly flexible spring migratory period that is associated with elevated energy reserves and, in captivity, nocturnal migratory restlessness. Beginning in May, male and female subjects were presented same-sex neighbors that were previously maintained on either a standard photoperiod (control neighbors) or a longer, summer photoperiod (photo-advanced neighbors, who exhibited more advanced reproductive development). We assessed the effect of these differing social cues on subjects over 28 days by monitoring nocturnal migratory behavior, body condition, and reproductive development. Subjects presented with photo-advanced neighbors ceased

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nocturnal migratory behaviors more rapidly than subjects paired with control neighbors. We also observed a relatively stronger response to social cues amongst female subjects. Rates of change in the body condition and reproductive development of subjects did not differ between treatment groups. This study provides novel insight into how social cues can influence migratory decision making and provides evidence of sex-specific differences in cue use.

KEYWORDS migration, social cues, settlement, decision-making, nomad, facultative migration

SIGNIFICANCE STATEMENT

Animals often use social information when making decisions. Less well understood is how the state of the information source influences social information use, particularly during migratory decision-making. Using a species of nomadic songbird, we experimentally demonstrate that the decision to terminate migratory behavior depends upon the state of nearby conspecifics. This study informs our understanding of how animals use social information to inform migratory decisions.

INTRODUCTION

Animals across the tree of life must make fitness-related decisions in the face of uncertainty (McNamara and Houston 1986). This uncertainty can surround a variety of behavioral decisions, including where and when to forage, who to mate with, whether to challenge competitors, and when to initiate or cease movement behaviors including dispersal and migratory behaviors. One way in which animals reduce the amount of uncertainty associated with these decisions is by using information obtained from their environment (Dall et al. 2005; Schmidt et al. 2010), including conspecific or heterospecific social information (Smith et al. 1999; Danchin et al. 2004; Couzin et al. 2005; Dall et al. 2005; Templeton and Greene 2007; Szymkowiak 2013). Though social information use has been documented in a variety of contexts, less well understood is to what extent the use of social information depends upon the state (e.g., age, life-stage, condition; McNamara and Houston 1996) of the source of social information (Helm et al. 2006; Németh and Moore 2014).

Numerous decisions must be made during animal migrations, often in the face of considerable uncertainty (Bauer et al. 2011; Németh and Moore 2014). For instance, animals must make departure decisions with little information on conditions at their distant destination. Similarly, animals may need to decide when and where to stopover en route, with limited opportunities to gather information about potential stopover sites. These migratory decisions are important to an individual's fitness as the timing of migratory arrival is associated with differences in survival (Lerche-Jørgensen et al. 2018) and reproductive success (Price et al. 1988; Smith and Moore 2005). Because decisions related to the timing of migratory events are associated with an individual's fitness, animal migrations provide a robust framework for assessing social information use in animal decision making. Though experimental field studies on migratory songbirds demonstrate that conspecific social information can attract birds to habitats normally avoided (Betts et al. 2008) and influence breeding site selection (Mukhin et al. 2008; Betts et al. 2008; Pärt et al. 2011; Morinay et al. 2020), previous studies cannot distinguish whether social cues influenced the termination of migration or habitat selection following the termination of migratory behavior (Ramenofsky and Wingfield 2006; Bauer et al. 2011; but see Robart et al. 2022).

Studies examining how migrants use social information have focused primarily on species that make regularly timed annual migrations to specific geographic areas (i.e., obligate migrants, Helm et al. 2006; Németh and Moore 2007) and much less well understood is to what extent species that exhibit alternative migratory strategies use social information. Nomadic migrants, for instance, make undirected and/or aseasonal movements either in response to fluctuations in resource availability or to find breeding habitats with abundant resources (Hahn et al. 2008; Watts et al. 2018; Teitelbaum and Mueller 2019). These nomadic movements can be highly variable in timing, distance, and direction and lead to low site fidelity (Newton 2012). Thus, nomadic migrants may not have a specific destination and frequently encounter unfamiliar environments (Teitelbaum and Mueller 2019). Because of the high degree of uncertainty associated with novel environments and unpredictable resource distributions, nomadic migrants are expected to rely heavily on local cues, particularly social information, in decision making (Watts et al. 2018; Teitelbaum and Mueller 2019). Indeed, social information has previously been found to influence the physiology of a migratory nomad in the context of unpredictable resource availability (Cornelius et al. 2010). However, relatively few studies have explored how and when nomadic migrants use social information to inform seasonal migratory decisions, including when to stop migrating.

Here, we experimentally test the hypothesis that the decision to terminate migration is influenced by social information and dependent upon the state of the information source using a captive population of a nomadic migrant, the pine siskin (*Spinus pinus*). Pine siskins are seasonally breeding, nomadic songbirds that frequently wander during the temperate spring and opportunistically breed upon discovering suitable habitats (Dawson 2020). Although pine siskins exhibit a temporally predictable window in spring when migratory behavior frequently occurs (Robart et al. 2018; Dawson 2020), they also show a high degree of flexibility in the expression of migratory behavior. For instance, both breeding and migratory individuals can co-occur in the same location (Yunick 1981; Dawson 2020; Cornelius et al. 2021). The vernal migratory period is characterized by physiological preparations and behavioral readiness for migration amongst captive individuals (Watts et al. 2017; Robart et al. 2018), making this species particularly well-suited to experimental studies. Moreover, previous work with captive pine siskins indicates that they are sensitive to the social environment towards the end of the vernal migratory period, with the presence of nonmigratory, male conspecifics causing declines in migratory behavior and body condition of migratory, male pine siskins (Robart et al. 2022). Thus, we can make use of this study system to test whether conspecific state influences social information use and whether the sexes differentially use social cues to inform migratory decisions. To this end, we presented captive male and female pine siskins with same-sex neighbors that were maintained on either a standard photoperiod (control neighbors) or a longer, summer photoperiod for two months prior to pairing (photo-advanced neighbors). This photoperiod manipulation was used to advance the neighbors in their annual cycle, as daylengths mediate life-stage transitions in many birds (Dawson et al. 2001), including pine siskins (Hahn et al. 2004; Robart et al. 2018). We used same-sex neighbors in this experiment as differences in the degree of affiliation in male-female pairs are known to influence female reproductive development in this species (Watts et al. 2016), and we sought to minimize this potential source of variation in the nature of social cues within treatment groups. Pine siskins frequently aggregate in mixed-sex groups (Watts, personal observation), and both same- and opposite-sex social cues are likely highly relevant. If the use of social information by pine siskins during the migratory settlement period depends upon the state of the information source, then we predict that subjects presented with photo-advanced

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neighbors will more rapidly transition from a migratory state into a breeding state because they are receiving social cues from neighbors that are further along in their annual cycle.

METHODS

Animals

Wild pine siskins were captured using either mist nets or baited funnel traps at multiple sites within Washington and Idaho (Conconcully, WA: 48.659, -119.841; Dayton, WA: 46.099, -117.786; Methow Valley, WA: 48.312, -120.279; Moscow, ID: 46.725, -117.003; Priest Lake, ID: 48.744, -116.837). For birds captured in breeding condition, sex was determined by the presence of either a brood patch or cloacal protuberance following (Pyle 1997). Birds captured in nonbreeding condition and birds hatched the same year of capture (i.e., hatch year birds) were genetically sexed using blood samples by the Washington Animal Disease Diagnostic Laboratory. At capture, birds were assigned an age of hatch year, after hatch year, or unknown by examining the extent of skull ossification and plumage characteristics (Pyle 1997). Birds aged as unknown were those that lacked obvious molt limits and were captured following the average date of complete skull ossification for hatch year birds (i.e., when both hatch year and after hatch year birds can have complete skulls). Following capture, birds were transported to Washington State University and initially housed in groups ranging from 15 to 25 individuals in one of 3 outdoor aviaries. While in captivity, including during the experiment described here, birds had *ad libitum* access to Roudybush Small Bird Maintenance Diet (Woodland, CA), a mixture of nyjer thistle and sunflower seed hearts, grit, and water. While indoors, except as noted below, birds were maintained on a photoperiod mimicking natural changes in day lengths at 47° N latitude, the same latitude as Pullman, WA.

A total of 28 birds were used as subjects in the experiment (n = 9 males, 5 females per treatment group). All subject birds were captured between June 2019 and November 2019. On February 10th, 2020, subjects were brought indoors and beginning March 10th, 2020 all subject birds were housed in individual cages (~34 x 38.5 x 43 cm) until the conclusion of the experiment. All rooms used for housing birds indoors were of similar size, directly adjacent to each other, outfitted with the same lighting, and maintained similar temperature and humidity profiles. Apart from two individuals that were after hatch year at capture, all subjects were captured as hatch year birds. We confirmed this difference in age did not influence our results by performing analyses with and without these two individuals. Subjects were assigned to the two treatment groups using a stratified random approach to balance groups as best as possible with respect to capture location, capture date, and initial nocturnal activity level.

An additional 56 birds were housed in same-sex pairs to serve as sources of social information (i.e., "neighbors", n = 18 males, 10 females per group) for the experiment. These 56 birds varied in their capture history as described in the Supplementary Material. Beginning in March 2020, all neighbors were housed in cages of the same size as subject cages and were moved into pairs in advance of Day 0 of the experiment. Within the two groups of neighbors, 39 individuals began the experiment as after-second year birds (i.e., they were initially captured as after hatch year birds) and 17 individuals were of unknown age. Individuals of unknown age were those that we were unable to distinguish them as hatch year or after-hatch year birds at capture. All unknown age birds were housed with a bird known to be after-second year, such that each pair of neighbors included at least one known after-second year bird. Neighbors were assigned to two groups using a stratified random approach to balance groups as best as possible based on capture location, capture date, and previous experimental experience.

Experimental Design

To experimentally manipulate the state of one neighbor group and thereby create the experimental social cues, the two groups of neighboring birds were maintained on different photoperiod regimes prior to presenting neighbors to subject birds. Control Neighbors were maintained on the same photoperiod as the subjects for the entirety of the experiment (i.e., mimicking that at 47° N). Photo-advanced neighbors were switched to an 18-hour daylength (18L:6D) for 48 days before pairing with the subject birds. This experimental day length is characteristic of daylengths in June in the northern breeding range limit of pine siskins. This photo-manipulation was designed to advance this group of neighbors in their annual cycle such that they transitioned from a vernal migratory state to a breeding state earlier.

Prior to Day 0, subjects were distributed between two rooms such that each room contained a mix of control and experimental subjects, and six nights of baseline data were collected (see Behavioral Data Collection and Condition Measurements below). On day 0 of the experiment (May 18th, 2020), all subject birds were moved to a new housing configuration (i.e., birds were moved between housing rooms) and were positioned adjacent to a cage housing two same-sex neighbor birds that were also the same sex as the subject. Birds belonging to the same treatment group were housed in the same room. Control subjects were randomly assigned to a set of control neighbors and experimental subjects were randomly assigned to a set of photo-advanced neighbors. Opaque dividers were used to visually isolated subjects from all other birds except their assigned neighbors. Subject birds could therefore only hear other subject and neighbor birds from the same treatment group and only see two neighbor birds of the same sex. Additionally, the positioning of subject and neighbor cages was such that limited physical interaction was possible between a subject and its assigned neighbors.

Behavioral Data Collection and Condition Measurements

Behavioral data and measures of body condition and reproductive development were collected to assess progress of birds through the stages of their annual cycle. Nocturnal activity, an indicator of a migratory stage (i.e., nocturnal migratory restlessness, (Berthold 1973; Gwinner and Czeschlik 1978; Watts et al. 2017), declines as birds terminate migration and transition to a breeding stage (Ramenofsky and Wingfield 2006). Body mass and fat, which are both elevated in birds during the vernal migratory stage (Berthold 2001; Robart et al. 2018; Cornelius et al. 2021), are also generally expected to decline as birds transition to a breeding stage, though short breeding windows, inclement weather on the breeding grounds, and preparing to reproduce can promote the maintenance of elevated body condition (Ricklefs 1974; Ramenofsky and Wingfield 2006). Indicators of reproductive readiness (cloacal protuberance length in males and brood patch development in females), on the other hand, should develop as birds transition to a breeding stage (Ramenofsky and Wingfield 2006). We did not assess changes in diurnal activity as pine siskins do not exhibit diurnal migratory restlessness during the spring migratory period (Watts et al. 2017; Robart et al. 2018).

We quantified nocturnal activity levels using passive infrared sensors (Starr Life Sciences Corp., Oakmonk, PA). Sensors were placed on top of each cage, attached to a VitalView Data

Acquisition System (Starr Life Sciences Corp., Oakmonk, PA). This position for sensors was chosen as it has previously captured nocturnal restlessness in this species (Watts et al. 2017; Robart et al. 2018). A small opaque divider was placed between the cages of each subject and their neighbor to prevent sensors from recording activity occurring in the adjacent cage. This divider was positioned on the lower half of the cage below the birds' perches and did not prevent subjects and neighbors from interacting or observing each other. We confirmed the barrier was tall enough to block the activity of neighbors by placing a caged bird adjacent to an empty cage with a sensor and verifying there was no activity detected by the sensor in the empty cage. Counts of activity were summed into 10-min bins. For subject birds, we calculated nocturnal activity levels by summing the total number of movements recorded between 2300 and 0300 of each night, a time window previously shown to include behaviors indicative of nocturnal migratory restlessness (Watts et al. 2017). For neighbor birds, collection of nocturnal activity began on day 0 when neighbors were presented to subjects. Because neighbors were housed in pairs and activity sensors measured the activity of both neighbors in a single cage, it was necessary to use a more coarse-grained measure of activity data. Specifically, the two birds in a cage were considered active if the number of movements within a 10-minute interval was greater than or equal to 20. Neighbor nocturnal activity levels were then quantified by summing the number of 10-minute bins between 2300 and 0300 during which the birds in a cage were considered active. This threshold-approach was used to reduce the amount of variation in the nocturnal activity associated with having two neighbors in a single cage. Over the course of the experiment, the activity of the 28 subjects and 28 cages housing neighbors were measured for

28 and 21 days which resulted in a total of 784 and 588 observations, respectively. Behavioral data were collected autonomously and therefore independent of observer bias.

We collected measurements of body condition and reproductive development of all subjects and neighbors 5 days before pairing (May 13th), a week after pairing (May 25th), two weeks after pairing (Jun 1st), and three weeks after pairing (Jun 8th). The body condition and reproductive development of each bird was therefore measured a total of 4 times over the course of the experiment. Measurements were made starting 2 hours after the time that the lights came on for a given measurement day. We assessed body condition by measuring body mass, furcular and abdominal fat deposits, and pectoralis muscle size. We measured body mass to the nearest 0.01g using an electronic balance. Furcular and abdominal fat were visually assessed on a scale from 0 (no fat) to 5 (bulging fat) and summed to generate a single fat score (Robart et al. 2018; Cornelius et al. 2021). Muscle size was visually scored from 0 (muscle concave with keel very prominent) to 3 (muscle bulging over keel, Bairlein 1995). We assessed male reproductive development by measuring the length of a male's cloacal protuberance, a sperm storage organ that seasonally enlarges in male songbirds (Hegner and Wingfield 1986). Female reproductive development was assessed by visually scoring the brood patch as follows: 0 (none, 0-20% defeathered), 1 (defeathering, 25-90% defeathered), 2 (defeathered, 95-100% defeathered), 3 (100% defeathered, fluid-filled), 4 (regressed but still 100% defeathered), and 5 (refeathering) as described in (Watts et al. 2016). One female subject in the control group was not measured at the first sampling prior to the start of the experiment. It was not possible to collect condition measurements blind to treatment group as all subjects belonging to a single treatment group were housed in the same room.

Statistical Analyses

All statistical analyses were performed in Program R v. 3.6.2 (R Core Team 2021). For all statistical analyses, we use a significance threshold of 0.05 and discuss effects with a p-value of < 0.1 as trends. We tested for pre-pairing differences (i.e., Days -6 to 0) between subject treatment groups and the effects of the neighbor group on subject nocturnal activity post pairing (i.e., Days 1 to 21) using generalized linear mixed models within the glmmTMB package (Brooks et al. 2017). For each of these analyses, we began by comparing two models. The first model included a continuous, fixed effect of experiment day, a categorical, fixed effect of treatment group, and a random intercept of individual ID. The second model included the same effects as well as an interaction between experiment day and treatment group. A nested ANOVA was used to determine if the model including the interaction term fit the data significantly better than the model without the interaction term using the *anova* function in R (Lewis et al. 2011). We then used the *emtrends* function within the *emmeans* package (Lenth 2020) to test if the slopes of the groups were significantly different from zero as well as each other. Lines of best fit and 95% confidence intervals for all GLMMs were generated using the *visreg* package (Breheny and Burchett 2017). We used this same analytical framework to test for sex-specific differences in the nocturnal activity of subjects by comparing support for a model with and without a three-way interaction between experiment day, treatment group, and sex. We tested for overdispersion and checked model assumptions using diagnostic tools in the *performance* package (Lüdecke et al. 2021) and the simulation approach within the DHARMa package in Program R (Hartig 2021). Diagnostic tests performed with the check_overdispersion function within the *performance* package identified the presence of overdisperson using a Poisson distribution. The simulated residual approach within the *DHARMa* package as well as a likelihood ratio test also identified better model fit using the negative binomial distribution. We therefore used the negative binomial distribution as opposed to the Poisson distribution for all generalized linear mixed models (O'Hara and Kotze 2010).

To examine the timing of any changes in each subject group's nocturnal behavior, we conducted a change point analysis using the *cpt.meanvar* function within the *changepoint* package (Killick and Eckley 2014). Change point analyses identify significant differences in mean activity levels if an added change point improves the log-likelihood of the model enough to overcome a penalty value that functions to prevent overfitting. We analyzed each treatment group separately to determine if nocturnal activity increased or decreased at different time points. We used the pruned exact linear time algorithm with a Poisson test statistic and a Bayesian Information Criterion penalty value. We identified weekly differences in mean activity by setting the minimum segment length to 7 days. The change point analyses conducted here could therefore identify a minimum of 0 and maximum of 4 change points for each treatment group. We included both pre- and post-pairing subject activity data in this analysis, though the minimum segment length of 7 days prevents the first change in activity from being detected until Day 0 of the experiment.

In addition to behavioral changes in response to the different social cues, we also tested if the social treatment influenced changes in body condition and reproductive development of control and experimental subjects. All three condition variables (i.e., fat score, muscle size, body mass) exhibited significant positive Pearson's correlation coefficients: r (upper, lower 95% confidence interval) for mass-fat: 0.74 (0.64, 0.81); muscle size-mass: 0.62 (0.49, 0.72); muscle size-fat: 0.59 (0.45, 0.70). We therefore used a principal component analysis with a covariance matrix to collapse three correlated metrics into a single index of body condition, the first principal component (hereafter 'body condition'). All three condition metrics loaded positively onto the axis of the first principal component (loadings for body mass = 0.58, fat scores = 0.79, and muscle size= 0.19) and the first principal component explained 85% of the variation. We examined the effects of our treatment on body condition and cloacal protuberance length (for males) using linear mixed models with a continuous, fixed effect of experiment day, a categorical, fixed effect denoting treatment group, an interaction between the experiment day and the treatment group, and a random effect of individual ID. Model residuals were examined to confirm assumptions of normality were met. For body condition, we quantified support for sex-specific changes by using an ANOVA to compare models with and without an interaction between the experiment day, treatment group, and sex. Analyses quantifying sex-specific changes in condition were included only if the ANOVA showed that including the sex interaction term significantly improved model fit. To test for effects of the treatment on the progression of brood patch development (an ordinal response variable) in females we used a cumulative link mixed model with the *ordinal* package (Christensen 2019). Fixed effects included in this model include experiment day, treatment group, and an interaction between experiment day and treatment group, and random effect of individual ID. As for activity data, we were also interested to test for pre-pairing differences in body condition and reproductive development. Since there was only one measurement of these variables prior to pairing, we evaluated this based on whether there was a significant additive effect of treatment in each model (with a significant effect indicating a difference between treatment groups prior to pairing).

Finally, we were also interested in comparing nocturnal activity, body condition, and reproductive development between photo-advanced and control neighbors to better understand differences in the social cues provided by neighbors to subjects. To understand potential differences between neighbor types, we used the same analytical approaches as described above for the subjects, but instead of treatment we used neighbor type (control or photo-advanced) as a fixed, categorical effect.

RESULTS

Subject Activity

For the period prior to pairing, a nested ANOVA did not support including the interaction term between treatment group and experiment day ($\chi^2 = 0.02$, p = 0.89, Supplementary Table 1). There were no differences detected in nocturnal activity between subject treatment groups prior to pairing ($\beta = 0.28$, p = 0.70, Fig. 1, Supplementary Table 1), nor did the post-hoc slope comparison identify differences in the change in activity pre-paring (t = -0.14, p = 0.89, Supplementary Table 1).

For the period post-pairing, a nested ANOVA supported the inclusion of the interaction between experiment day and treatment group in the model for nocturnal activity ($\chi^2 = 20.57$, p < 0.0001, Supplementary Table 2A) and the interaction between experiment day and treatment was significant ($\beta = 0.08$, p < 0.0001, Supplementary Table 2B). Experimental subjects exhibited significant decreases in their daily nocturnal activity over the course of the post-pairing period ($\beta = -0.06$, p = 0.0007, Fig. 2A, Supplementary Table 2C). Control subjects exhibited increases in their daily nocturnal activity that approached the significance threshold of 0.05 ($\beta = 0.02$, $p = 0.08$, Fig. 2A, Supplementary Table 2C). Post hoc slope comparisons revealed that the groups exhibited significantly different changes in their nocturnal activity after being paired with neighbors ($t = -4.58$, $p < 0.0001$, Supplementary Table 2D). Change point analyses further revealed similar differences between the subjects of each group in the timing and directionality of the changes in weekly nocturnal activity (Fig. 1). We therefore observed similar effects of the contrasting social cues on nocturnal activity using two separate analytical approaches.

There were no sex-specific differences in nocturnal activity prior to pairing (Fig. 1, Supplementary Table 3). Post-pairing, the nested ANOVA comparing the models with and without the sex interaction term supported inclusion of the sex interaction in the model ($\chi^2 = 9.93$, $p = 0.02$, Supplementary Table 4A). Post hoc slope comparisons revealed that among experimental subjects, females tended to exhibit greater declines in nocturnal activity than did males (estimate = -0.07, $t = -2.45$, $p = 0.07$, Fig. 2B, Supplementary Table 4D). Female control subjects exhibited significant increases in nocturnal activity over the course of the experiment, while males exhibited no change in nocturnal activity ($\beta_{females} = 0.05$, $p = 0.02$; $\beta_{males} = 0.01$, $p = 0.82$, Fig. 2B, Supplementary Table 4C). Post hoc slope analyses showed that experimental and control females exhibited significantly different changes in daily nocturnal behavior (estimate = -0.16, $t = -5.28$, $p < 0.0001$, Supplementary Table 4D), though the two groups of males did not exhibit significantly different changes in daily nocturnal activity (estimate = -0.04, $p = 0.18$, Supplementary Table 4D). Change point analyses revealed similar sex-specific differences in the daily nocturnal activity of subjects (Fig. 1C-D). We therefore documented sex-specific effects of the contrasting social cues on nocturnal activity using two separate analytical approaches.

Subject Body Condition

The two subject groups unexpectedly differed in body condition when the experiment began, with experimental subjects exhibiting significantly lower values of condition than control subjects ($\beta = -2.47$, $p = 0.01$, Supplementary Table 5B). This difference was observed even though birds from both treatment groups were housed together during the pre-pairing period and assigned to treatment groups using a stratified random approach. Body condition declined over the course of the entire experiment ($\beta = -0.11$, $p < 0.001$, Supplementary Table 5B, Fig. 3A), independent of treatment group (experiment day x treatment group interaction = 0.04, $p = 0.27$, Supplementary Table 5B). The nested ANOVA comparing the body condition models with and without the sex interaction term did not support the inclusion of the sex interaction in the model ($\chi^2 = 4.89$, $p = 0.3$, Supplementary Table 5A).

Subject Reproductive Development

Males did not exhibit differences in their cloacal protuberances at the start of the experiment ($\beta = 0.04$, $p = 0.89$, Supplementary Table 5D). Males did exhibit increases in the length of their cloacal protuberance ($\beta = 0.05$, $p < 0.0001$, Fig. 3B), but the interaction between experiment day and treatment group was not significant ($\beta = -0.01$, $p = 0.32$, Supplementary Table 5D). The extent of female brood patch development did not differ between treatment groups during the pre-paring period ($\beta = 2.19$, $p = 0.32$, Supplementary Table 5C). Female brood patches did develop over the course of the experiment ($\beta = 0.51$, $p < 0.0001$, Fig. 3C), though the rate of development did not depend upon the treatment group ($\beta = -0.12$, $p = 0.13$, Supplementary Table 5C).

Effect of Subject Body Condition on Nocturnal Activity

Because of the unexpected significant difference in the body condition index at the beginning of the experiment between the two subject groups, we further assessed if an individual's condition at the beginning of the experiment influenced the relationship between the treatment group and nocturnal activity over the course of both the pre- and post-pairing period. We used the same modeling approach described above but added a predictor variable indicating a bird's body condition at the beginning of the experiment. Specifically, we used a generalized linear mixed model with a negative binomial distribution in which the response variable was the daily nocturnal activity of the subjects and predictors included a fixed, categorical effect of treatment, a fixed, continuous effect of experiment day, an interaction between experiment day and the treatment group, a fixed, continuous effect of a subject's body condition at the beginning of the experiment, and a random effect of individual ID. The effect of the treatment group remained ($\beta_{\text{experiment day}} = -0.06$, $p < 0.0001$, $\beta_{\text{experiment day * treatment group}} = 0.05$, $p < 0.0001$) despite the trend of a bird's initial body condition on nocturnal activity ($\beta = 0.13$, $p = 0.09$).

Evaluating Differences Between Neighbor Groups

The nested ANOVA did not support including an interaction between experiment day and type of neighbor group ($\chi^2 = 1.37$, $p = 0.24$, Supplementary Table 6A). Though neighbors did exhibit declines in daily nocturnal activity ($\beta = -0.03$, $p = 0.0002$, Supplementary Table 6B, Fig. 4A), the additive effect of neighbor group type was not significant ($\beta = 0.22$, $p = 0.75$, Supplementary Table 6B), nor was the interaction term significant ($\beta = 0.01$, $p = 0.24$, Supplementary Table 6B). Post hoc analyses of the slopes of each group revealed that photo-advanced neighbors exhibited a significant decline in nocturnal activity ($\beta_{\text{photo-advanced neighbors}} = -0.03$, $p = 0.0003$, Supplementary

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Table 6C) and control neighbors showed a trend of declining activity ($\beta_{\text{control neighbors}}$ = -0.01, p = 0.06, Supplementary Table 6C), though the two slopes were not significantly different (estimate = -0.01, t = -1.17, p = 0.24, Supplementary Table 6D). The nested ANOVA comparing models with and without the sex interaction term supported the inclusion of the interaction term (χ^2 = 14.65, p = 0.002, Supplementary Table 7A, Fig. 4B-C). Post-hoc analyses of the slopes of each group revealed that females in both groups exhibited significant declines in nocturnal activity ($\beta_{\text{photo-advanced females}}$ = -0.08, p < 0.001; $\beta_{\text{control females}}$ = -0.03, p = 0.02, Supplementary Table 7C) whereas males did not exhibit significant declines in activity ($\beta_{\text{photo-stimulate males}}$ = -0.02, p = 0.1; $\beta_{\text{control males}}$ = -0.01, p = 0.94, Supplementary Table 7C), as was observed in the subjects. Further post hoc comparisons of the treatment-specific slopes of each sex revealed no significant differences in changes in nocturnal activity between treatment groups (t_{females} = -2.07, p = 0.16; t_{males} = -1.00, p = 0.75, Supplementary Table 7D). These results indicate that the two groups of neighbors did not exhibit significant cage-level differences in their nocturnal activity at the start of the experiment, nor did they exhibit significantly different cage-level changes in their activity over the course of the experiment post-pairing.

Neighbor groups did not exhibit significant differences in body condition at the beginning of the experiment (β = 0.27, p = 0.67, Supplementary Table 8B). The nested ANOVA comparing the body condition models with and without the sex interaction term did not support the inclusion of the sex interaction in the model (χ^2 = 4.71, p = 0.32, Supplementary Table 8A). Neighbors of both groups exhibited significant declines in condition over the course of the experiment (β = -0.06, p < 0.0001, Supplementary Table 8B, Fig. 5A), though the interaction

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between the day of the experiment and treatment group was not significant (β = -0.02, p = 0.23, Supplementary Table 8B).

Males of both groups of neighbors did not exhibit significant differences in cloacal protuberance length at the start of the experiment (β = 0.12, p = 0.54, Supplementary Table 8C), but did exhibit significant increases in cloacal protuberance length over the course of the experiment (β = 0.03, p < 0.0001, Supplementary Table 8C, Fig. 5B). The interaction between experiment day and treatment group was significant (β = -0.02, p = 0.01, Supplementary Table 8C), indicating that male control neighbors exhibited faster increases in cloacal protuberance lengths than photo-advanced neighbors (Fig. 5B). Photo-advanced female neighbors exhibited more advanced brood patch development at the beginning of the experiment (β = 4.05, p = 0.046, Supplementary Table 8D, Fig. 4C). Across both neighbor group types, females developed their brood patch over the course of the experiment (β = 0.38, p < 0.0001, Supplementary Table 8D, Fig. 5C). The interaction between experiment day and treatment group approached the significance threshold of 0.05 (β = -0.12, p = 0.08, Supplementary Table 8D). This trend for control neighbors to develop their brood patch faster than photo-advanced females could reflect observed differences in brood patch development between neighbor groups at the start of the experiment.

DISCUSSION

This study provides experimental evidence that the response to social information in the context of migratory decision-making depends upon the state of the information source in a nomadic songbird. We found that changes in nocturnal behavior, indicative of migratory termination, differed between birds with photo-advanced neighbors and those with control neighbors. Specifically, birds with photo-advanced neighbors reduced their nocturnal migratory restlessness more rapidly than control birds. Previous studies focusing on decision making in the contexts of foraging and predator avoidance have shown that characteristics of the information source can mediate social information use (Clay et al. 2012; Rauber and Manser 2018); here we demonstrate that this also occurs in the context of migratory decision-making.

During the transition from a migratory to breeding life stage, the reproductive systems of many species begin to develop and energetic reserves typically decline from those levels observed during the migratory period (Ramenofsky and Wingfield 2006). In this study, although the social treatment influenced nocturnal migratory restlessness, we saw no effect of treatment on body condition or reproductive development. Subjects in both control and treatment groups showed similar declines in body condition and similar rates of reproductive development, though we note that sample sizes for females were relatively small (n = 5 per group). Thus, our results suggest that pine siskins can adjust migratory behavior independently from body condition or reproductive development during the vernal period in response to supplementary cues such as social information. This flexibility may reflect the high degree of overlap in the timing of migration and breeding stages in this species (Cornelius et al. 2021), and may be a common characteristic of nomadic migrants more generally. On the other hand, even obligate migrants maintain a degree of flexibility during the migration-breeding transition in case environmental conditions deteriorate and they need to resume migration (Ramenofsky and Wingfield 2006). Thus, such flexibility could be a more general feature of the migration-breeding transition across migratory forms.

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In seasonally breeding birds, photoperiod as well as a suite of supplementary cues, including social cues, can mediate the transition between different life-history stages, including reproductive development (Dawson et al. 2001; Chmura et al. 2020). However, cue use is thought to differ between the sexes (Coppack and Pulido 2009; Chmura et al. 2020), with females being more dependent upon supplementary cues indicative of favorable conditions compared to males (Ball and Ketterson 2008; Watts et al. 2016). For instance, in mountain white-crowned sparrows (*Zonotrichia leucophrys gambelii*), females, but not males, have been found to alter pre-migratory fattening in response to temperature cues (Wingfield et al. 1996). In the current study, females showed greater behavioral responsiveness than males to the experimental supplementary cues of the photo-advanced neighbors. These behavioral differences provide new evidence of sex-specific differences in supplementary cue use during the migratory period (Chmura et al. 2020). Such sex-specific differences in cue use for migratory decision-making may contribute to the commonly observed pattern of protandrous migration in birds (Coppack and Pulido 2009). As supplementary cues reflect local environmental conditions in the immediate term, our results also support the hypothesis that cue use by females is shaped by fecundity selection, while male cue use is a product of sexual selection (Ball and Ketterson 2008; Coppack and Pulido 2009). Although beyond the scope of this study, age or experience could also influence the use of social cues (Chernetsov et al. 2004; Németh and Moore 2014). The subjects in our experiment were almost all second-year birds, and thus may have been more sensitive to social cues than older and more experienced birds.

Determining the salient information within social cues is central to our understanding of social information use. In the context of reproductive decision-making, conspecific social cues are proposed to convey information about habitat quality and the availability and state of potential mates (Szymkowiak 2013; Chmura et al. 2020). Here, our comparison of the two groups of neighbors suggests that the differences in the information encoded within social cues from these groups may have been associated with differences in reproductive development rather than nocturnal activity. However, our ability to evaluate the behavior of neighbors was limited by having only cage-level, rather than individual, activity data. More generally, we measured only a subset of myriad behavioral and physiological traits that may have differed between the two groups of neighbors. Thus, we cannot rule out that undetected differences between neighbor groups, in nocturnal activity or other attributes (e.g., vocal or olfactory cues, Grieves et al. 2019; Bentley et al. 2000), contributed to the behavioral differences amongst subject groups. Finally, in addition to cues from their same-sex neighbors, subjects may also have gathered information from opposite sex subjects and neighbors in the same treatment group via acoustic and/or olfactory pathways. Thus, we can't rule out the possibility that social cues from opposite-sex birds elsewhere in the room also influenced the behavioral responses observed. Indeed, amongst free-living animals, cues from breeding pairs are likely important in migratory decision making (e.g., Kelly and Ward 2017), though it is not clear if such cues promote or discourage the termination of migratory behavior, particularly in nomadic species. We also note that age or experience is another aspect of the state of the source of information (i.e., neighbors in the context of this experiment) that could influence response. The current study was not designed to explore this possibility, but this could be a promising avenue for future research.

The reproductive success of migratory animals often depends upon the quality of the breeding habitat in which they settle (Rodenhouse and Holmes 1992; Nagy and Holmes 2005;

Ware and Thomson 2005; Kubelka et al. 2022). Locating high quality breeding habitat may pose a particular challenge for nomadic migrants that exhibit low site fidelity and depend upon breeding resources that are highly variable in space and time (Koenig and Knops 2001; Stojanovic et al. 2015; Teitelbaum and Mueller 2019; LaMontagne et al. 2020). Our results highlight the importance of social cues for nomadic migrants, particularly females, deciding when to stop migrating in the spring and suggest that social cues may be a reliable indicator of high-quality breeding habitat for nomadic migrants. More broadly, this study demonstrates the utility of experimental studies of migratory animals for advancing our understanding of cue use in animal decision-making.

DECLARATIONS

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COMPETING INTERESTS - The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY – Data and code used to produce results are available through the Washington State University Research Exchange: https://doi.org/10.7273/000003927

ETHICS APPROVAL- All applicable national and institutional guidelines for the use of animals were followed. Birds were collected under scientific permits from the US Fish and Wildlife Service,

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Washington Department of Fish and Wildlife and Idaho Fish and Game. All procedures were approved by the Washington State University Institutional Animal Use and Care Committee (protocol: 6082).

AUTHOR CONTRIBUTIONS - HEW, JMC, and BJV designed the study; BJV collected, analyzed, and visualized the data; BJV wrote the first draft of the manuscript and all authors edited subsequent drafts.

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Fig. 1 Changes in nocturnal activity levels during the migratory settlement period in subjects paired with photo-advanced neighbors (experimental) or control neighbors (control). Colored lines show significant changes in mean nocturnal activity as identified by change point analyses. Solid and dashed black lines denote changes in daily, mean activity levels, and gray bands depict standard error. **A** and **B** depict treatment group changes in activity, while sex-specific changes in activity are shown in **C** (control) and **D** (experimental). Subject birds were paired with neighbors on Day 0.

Fig. 2 Changes in daily nocturnal migratory behavior over the course of the migratory settlement period in subjects paired with neighbors of the same sex that were either photo-advanced (experimental) or control. Group-specific lines of best fit and 95% confidence bands derived from the generalized linear mixed models are shown for all (A) subjects and (B) male and female subjects. Model summaries can be found in Supplementary Tables 1 and 2, respectively.

Fig. 3 Physiological changes in subject birds paired with photo-advanced neighbors (experimental) or control neighbors (control). **A**) Changes in the body condition index. **B**) Changes in male cloacal protuberance length. Thick lines in **A** and **B** reflect group-level trendlines while thinner, faded lines show individual measurements. **C**) Changes in female reproductive development as indicated by the progression of brood patch development. Summaries of the associated linear mixed models can be found in Supplementary Table 5.

Fig. 4 Daily nocturnal activity level over the course of experimental period in photo-advanced and control neighbor pairs. Group-specific lines of best fit and 95% confidence bands derived from the generalized linear mixed models are shown for all (A) neighbor pairs and (B) male and female neighbor pairs. Model summaries can be found in Supplementary Tables 3 and 4, respectively.

Fig. 5 Physiological measures in photo-advanced and control neighbors across the experimental period. **A**) Body condition index. **B**) Male cloacal protuberance length. Thick lines in **A** and **B** reflect group-level trendlines while thinner, faded lines show individual measurements. **C**) Female reproductive development as indicated by brood patch development. Summaries of the associated linear mixed models can be found in Supplementary Table 6.

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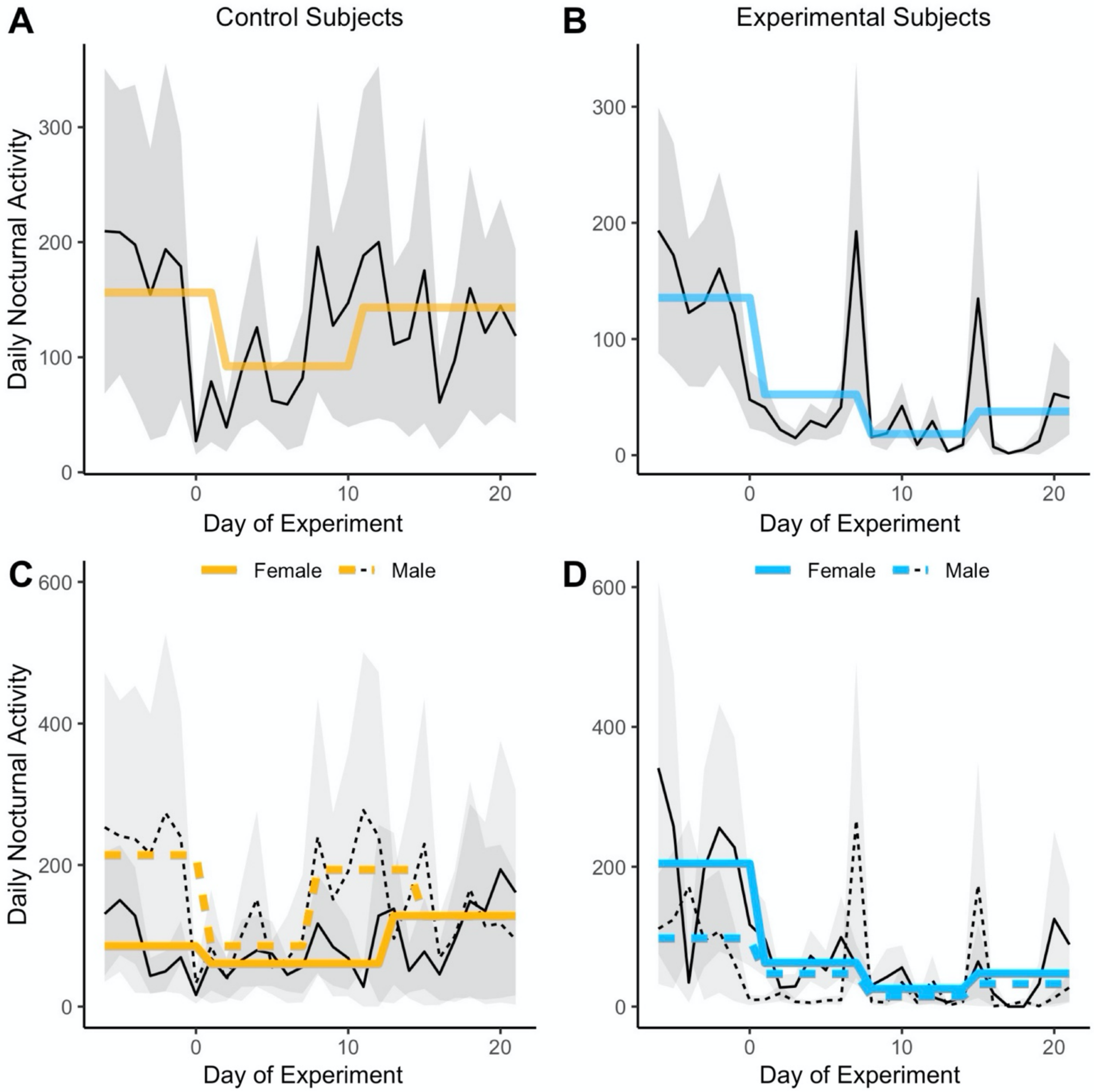
Figure 1.



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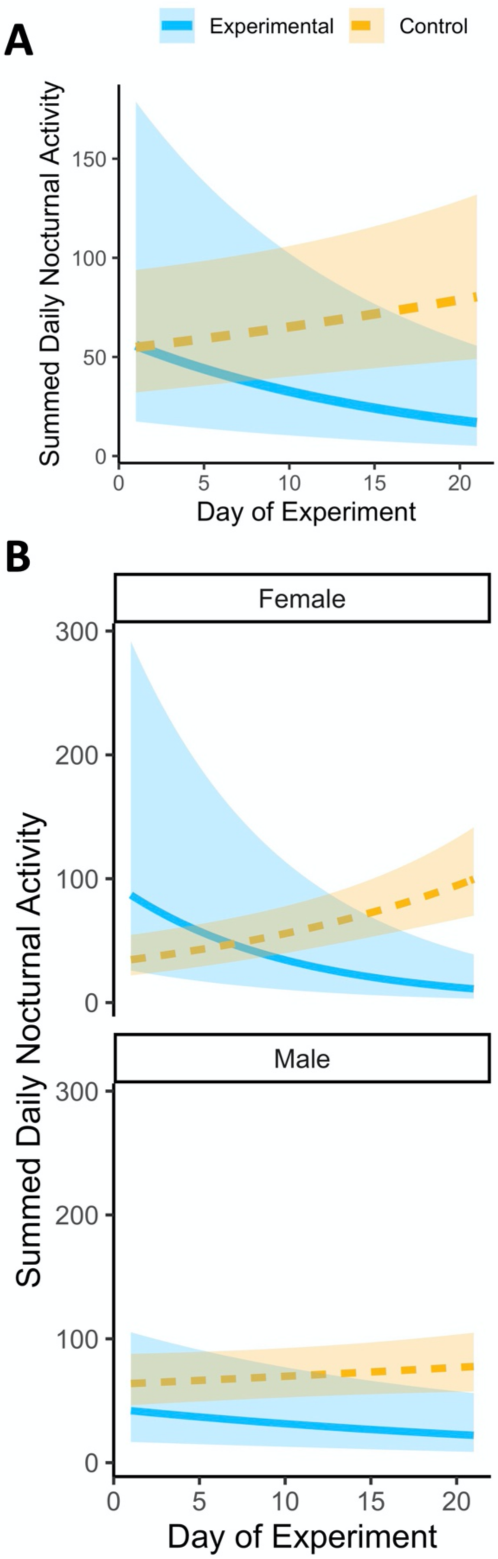
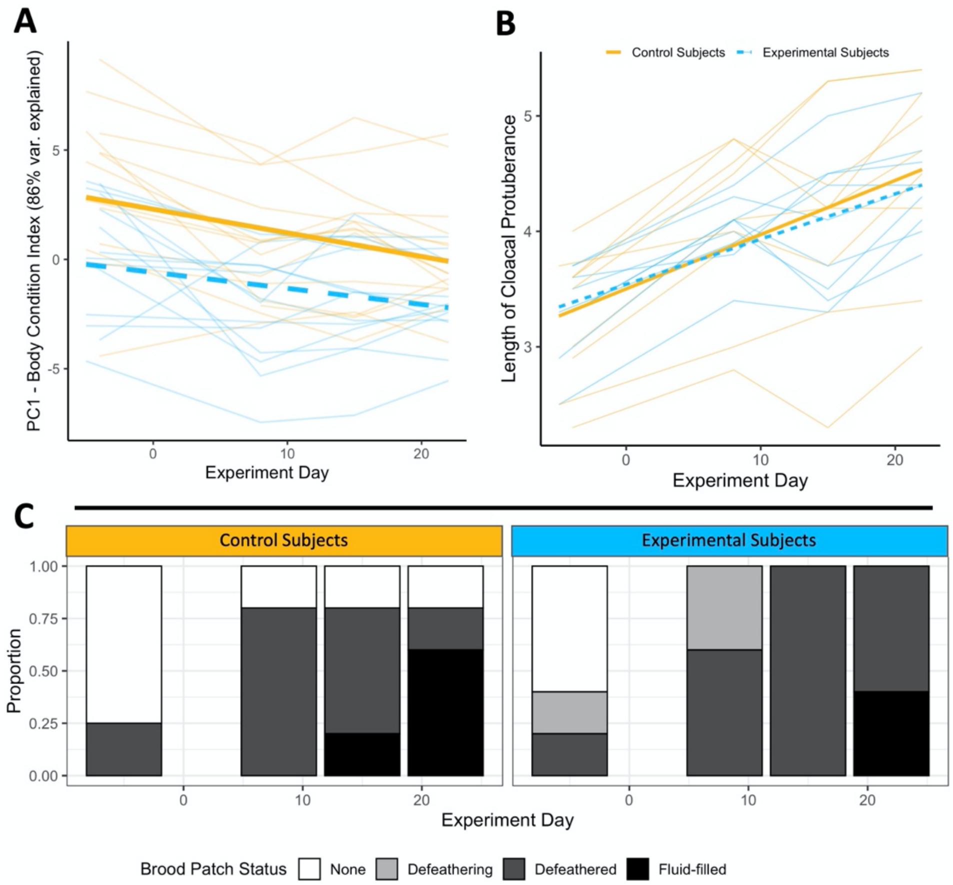
744 **Figure 2.**



745

Figure 3.


A
PC1 - Body Condition Index (86% var. explained)
5
0
-5
0
10
20
Experiment Day
B
Control Subjects
Experimental Subjects
Length of Cloacal Protuberance
5
4
3
0
10
20
Experiment Day
C
Control Subjects
Experimental Subjects
Proportion
1.00
0.75
0.50
0.25
0.00
0
10
20
0
10
20
Experiment Day
Brood Patch Status
None
Defeathering
Defeathered
Fluid-filled

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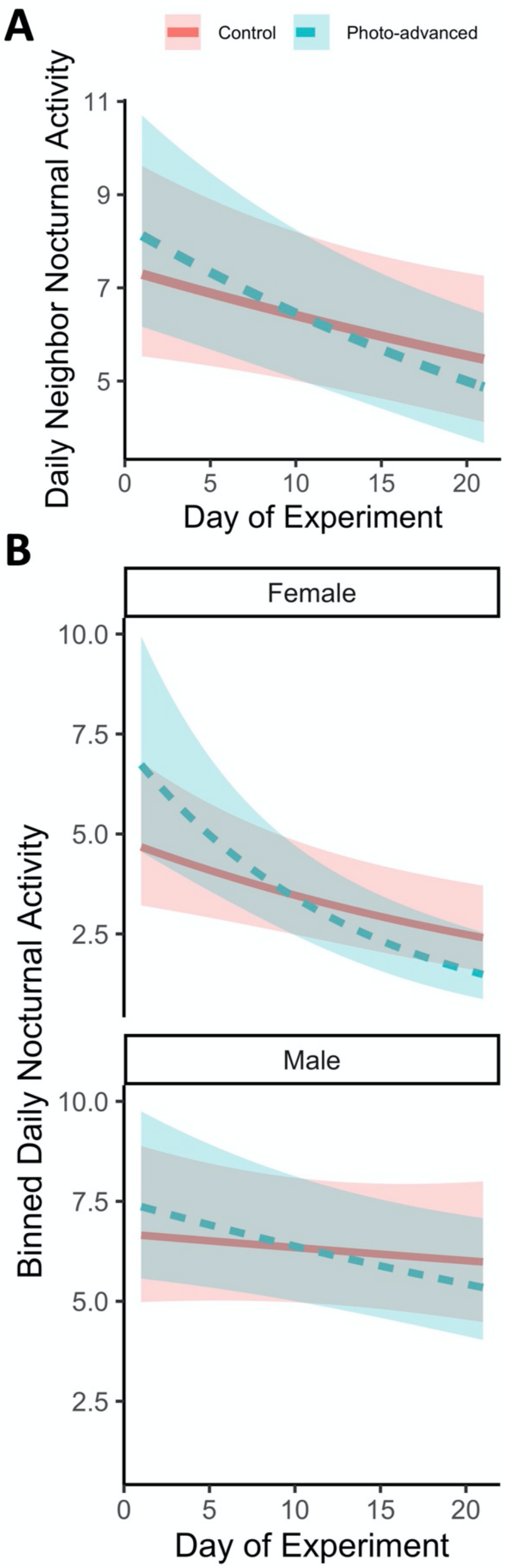
750 **Figure 4.**



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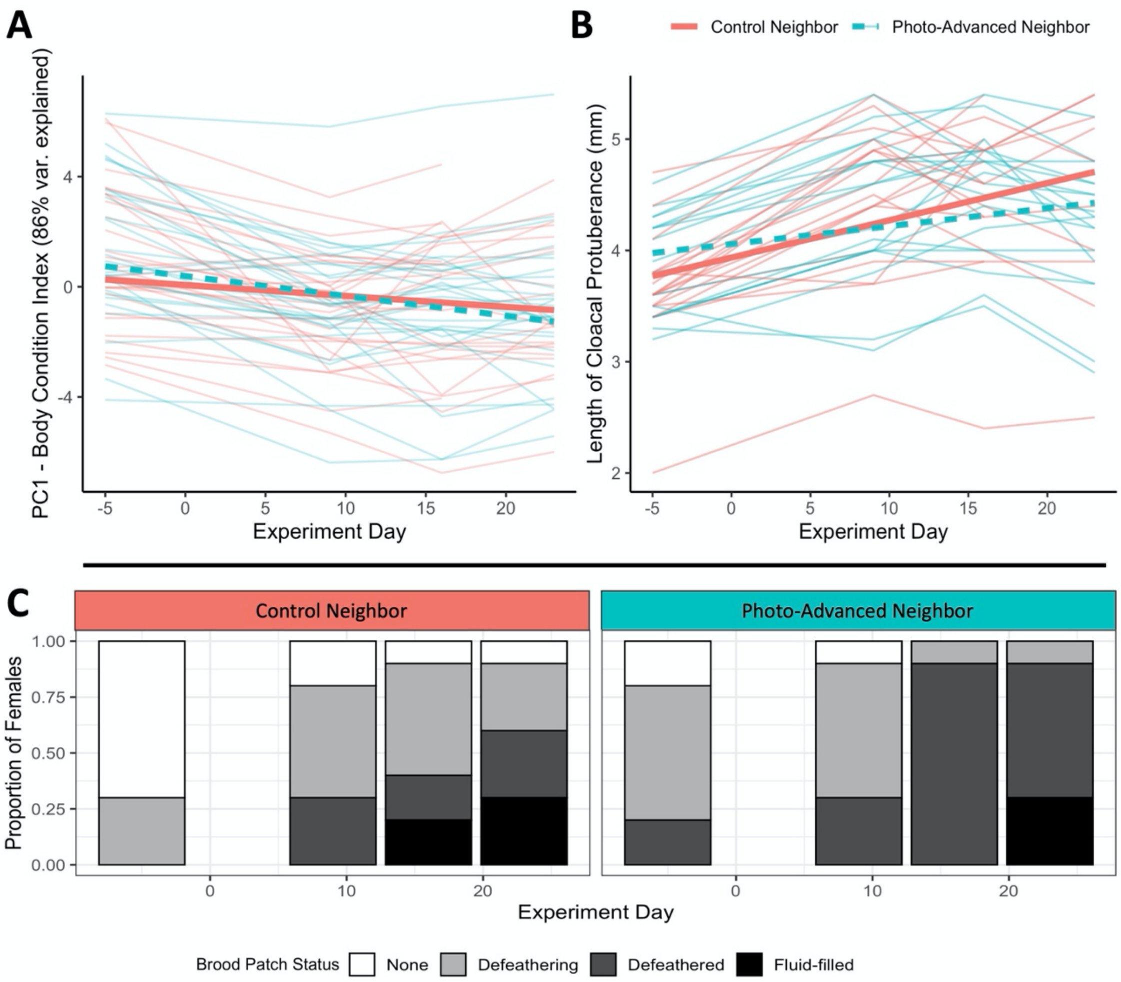
753 **Figure 5.**



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