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Influence of social cues on the initiation of migratory behavior in red crossbills (Loxia curvirostra)

John Bobo

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Influence of Social Cues on the Initiation of Migratory Behavior in Red Crossbills (*Loxia curvirostra*)

by

John Bobo

Thesis

Submitted to the College of Arts and Sciences
Eastern Michigan University
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MASTER OF SCIENCE
in
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Abstract

The timing of migration is crucial for the fitness of organisms because mistimed migration can cause exposure to difficult conditions. Photoperiod drives migratory timing in many species, but little work has focused on how social cues might fine-tune migratory timing. The goal of this study is to determine if birds use social cues from conspecifics to fine-tune the initiation of migratory behavior and physiology. Red crossbills (*Loxia curvirostra*) are gregarious, nomadic migrants that make seasonal movements to find patchily-distributed conifer seeds and are responsive to social cues in the context of food. I test the hypothesis that social cues can influence migratory timing in red crossbills by providing birds with social partners in different migratory states and measuring the development of migratory traits. We discuss the changes observed in body condition and activity levels to test the hypothesis that crossbills are using social cues from conspecifics to fine-tune migratory timing.
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Background

The Migratory Spectrum

One of the most widely recognized natural phenomenon is the collective migrations of thousands of different species across many different taxa. From butterflies to songbirds to whales, within almost every group of animals there are species that make predictable movements around the world in pursuit of food, habitat, and mates (Alerstam et al., 2003). The nature of migratory behavior is not consistent across taxa—some species display highly predictable and repeatable migratory behaviors, and other species perform migrations that are unpredictable in both time and space. Migration and the associated physiology and behavior may be best considered a spectrum, with the two ends being obligate or facultative in nature (Berthold, 2001). Obligate migration is characterized as being regular, consistent, and predictable. Obligate migrants leave and return to the same breeding habitats every year, sometimes even with incredible spatial precision, at the same time of year and with little variability between years (Newton, 2012). Obligate migrants thus rely on endogenous circannual rhythms and photoperiodic cues to prepare for and time migrations. Facultative migration, on the other hand, is used to broadly describe migratory behaviors that do not display the same level of predictability as obligate migration (Newton, 2012). These movements can be seasonal or temporally unpredictable and can occur on small or large scales to bring animals into new habitats (Ramenofsky et al., 2012). For facultative migrations that are temporally predictable, as is the case with some seasonal nomadic migrants, predictive timing mechanisms such as endogenous rhythms and photoperiod may play an important regulatory role. However, facultative migrants probably rely on a wider range of environmental cues to initiate movements.
between habitats given the higher degree of spatial and temporal variability (Ramenofsky et al., 2012).

**Physiological Preparations for Migration**

Despite differences in the migratory behavior itself, many of the physiological preparations a bird may undertake to prepare for long-distance flight remain similar. In many cases, muscle hypertrophy can be observed, particularly in the skeletal muscles used to power flight (Ramenofsky & Wingfield, 2007). This hypertrophy aids in long-distance flight endurance and can also be a fuel and water source via catabolism (Ramenofsky & Wingfield, 2007). Most energy for flight, however, is thought to come from lipids, which are hydrophobic and are therefore a much lighter way to store fuel than are proteins. An observed increase in fat deposition is regarded as a hallmark sign of migratory preparation in birds (King & Farner, 1959). Large fat deposits provide a reliable energy source for the bird during migration and is often accomplished through a combination of changes in physiology and behavior (e.g., hyperphagia; Odum, 1960). Subcutaneous fat deposits and muscle condition can be scored visually through the skin of small songbirds and allows for quantification of changes in body condition related to the transition to the migratory stage (Weise, 1967; Jenni-Eiermann & Jenni, 1996; Landys et al., 2004; Holberton et al., 2008; Fusani et al., 2009). The increase in fat deposits and muscle hypertrophy combine to cause an overall increase in mass of the bird prior to migration (Ramenofsky et al., 1999). Birds must contend with the trade-offs associated with increased mass due to fat deposition and muscle hypertrophy and the impact of added mass on flight dynamics (Lindstrom & Alerstam, 1992). For example, a fatter bird requires more power to maintain flight but also has a larger flight range (Blem, 1976). There is therefore an upper limit to the size of fat deposits due to flight-mechanic constraints (Lindstrom & Alerstam, 1992).
and birds will optimize the amount of fat deposits depending on their migratory flight needs (Lindstrom & Alerstam, 1992).

**Behavioral Changes During Migration**

Hyperphagia is an important driver of increased fat deposition in migrants, but it may also be a useful behavioral indicator of migratory preparations associated with migration in captive and wild birds (King & Farner, 1959). Similarly, changes in activity of caged birds can indicate a migratory state in birds. Migratory restlessness refers to the perch-hopping activity displayed by a captive bird which coincides with the migratory period of their wild conspecifics (Wagner, 1930; Gwinner & Czeschlik, 1978). Migratory restlessness is often used as a proxy for migratory behavior in birds and appears to mirror within-individual and species level variation in migratory behavior (Eikenaar et al., 2014). For example, northern wheatears (*Oenanthe oenanthe*) that display a lower level of migratory restlessness were more likely to remain at stopover sites the following night compared to individuals with higher levels of migratory restlessness (Eikenaar et al., 2014). Thus, changes in observed activity levels in captive birds may signal the initiation of migratory behavior. Migratory restlessness has primarily been described in obligate migrants, but facultative migrants may also exhibit migratory restlessness (Watts et al., 2016). Pine siskins (*Spinus pinus*) housed in captivity with a naturally occurring photoperiod increased nighttime activity coincident with the migratory period often seen in wild birds (Watts et al., 2016). Many facultative migrants move during the day—presumably to assess resource condition as they move (Newton, 2006); thus, it may be more difficult to detect migratory transitions in such species in captivity. Captive facultative migrants have shown increased diurnal activity in the context of declining food (Cornelius et al., 2010) and may even show diurnal increases in activity during seasons when movements are common even if food is
abundant (Watts et al., 2016). Food intake may thus coincide with pre-migratory mass gains whereas activity may indicate the actual behavioral transition into a migratory state.

**Cues Influencing Migration**

For most organisms, the migratory life stage is regulated by both internal and external cues (Bauer et al., 2011). Photoperiod, or the change in daylength, is an external cue which is known to have a very strong effect on migratory timing in birds because it is a reliable indicator of seasonal environmental change (Bauer et al., 2011). Birds are known to use the annual cycle of photoperiod changes as a long-term predictive cue to ensure the timing of different life-history events (i.e., breeding, molting, migration). Photoperiod entrains biological rhythms and can thus influence the onset of migratory restlessness in many passerines (Gwinner, 1990) and waterfowl (Newton, 2008). These internal and external cues interact to ensure the behavioral and physiological preparations displayed by facultative and obligate migrants occur at the appropriate time of the year (Newton, 2012). Migratory timing mechanisms can be considered as flexible reaction norms: A genetically influenced “migratory threshold,” which is an internal cue that initiates migratory preparation, is entrained by photoperiod and can also be influenced by local environmental cues such as food availability or social cues. The internal and external migratory cues experienced by the bird are therefore interacting with one another to better fine-tune the migratory behavior of the bird (Newton, 2012).

The impact of social cues on migratory behavior or physiology has been observed in a diverse range of taxa, but most research has investigated how social cues are used when making navigational or settlement decisions or how social status affects individual migratory behavior during a collective migration. Wetland birds, for example, are known to use social cues and information about previous reproductive success to make decisions about habitat selection during
migration (Ward et al., 2010). American redstarts use songs and social cues from conspecifics to settle and select breeding territories (Hahn & Silverman, 2006). Yellow-breasted chats use the nocturnal songs of conspecifics to make decisions about stopover habitat during migration (Alessi et al., 2010) and passerine migrants in the Gulf of Mexico have been observed participating in feeding assemblages, possibly as a way of quickly gathering information about an unfamiliar habitat (Németh & Moore, 2007). Less work has focused on how social cues might impact the initiation of migratory behavior. One study, however, found that non-migratory captive silvereyes (Zosterops lateralis) housed in the same room as migrants were more likely to display migratory restlessness the following day than non-migratory captive birds that were housed in isolation (Chan, 1994). Social cues may therefore be important for decision-making during migration and may allow birds to adjust migratory timing.

**Knowledge Gaps**

Research investigating the role of different environmental cues on facultative migration is far behind that of obligate migration, due in part to the difficulty of studying birds which display highly variable behaviors (Hochachka et al., 1999). The literature suggests that the continued decline in the conservation status of irruptive migrant species is not due to our lack of action but rather to our lack of knowledge (Cottee-Jones et al., 2016), further highlighting the need to deepen our understanding of the nuances of facultative migration. More broadly, the timing of life history stages to optimally match favorable environmental conditions is crucial to the fitness of an organism—especially migration (Thomas et al., 2001; Smith & Moore, 2005). While there is a rich body of work on the role of social cues in the timing of reproduction (Hau et al., 2008), work on how social cues may impact the initiation and timing of migration is lacking for both obligate and irruptive migrants—despite the social nature of birds and the theoretical and
empirical work suggesting the importance of social cues to migratory initiation (Hamilton, 1962; Chan, 1994; Bazazi et al., 2010; McNamara et al., 2011; Németh & Moore, 2014).

The goal of this research is to examine how social cues affect or influence the timing of migratory behavior and the migratory life stage of a facultative migrant. I test the following hypothesis: Birds use social cues from conspecifics to fine-tune the initiation of migratory behavior and physiology. If birds are using social cues to fine-tune the timing of migration, I predict that the presence of migratory conspecifics will advance the onset of migratory restlessness and the increase in body condition associated with migration in non-migratory birds relative to birds who are paired with non-migratory conspecifics.

**Study System**

Red crossbills (*Loxia curvirostra*) are highly facultative migrants that are nomadic, gregarious, and specialize on a very patchy resource, conifer seeds (Benkman et al., 2019; Newton, 2006a; Dawson, 2014). Previous studies of the species have found effects of social cues on their physiology and behavior, suggesting that social cues are utilized to make decisions or influence the decision-making process at an individual or group level (Cornelius, 2009; Sewall & Hahn, 2009; Cornelius et al., 2010; Cornelius & Hahn, 2012; Watts et al., 2016). For example, captive crossbills housed next to food restricted neighbors respond more strongly to changes in food availability than those housed next to birds with free access to food (Figure 1).

Red crossbills only reproduce if the seed crop in a particular year is sufficient (Newton, 1967; Benkman, 1993; Benkman et al., 2019). The spatial distributions and movement patterns of the red crossbill are closely tied to the distribution of conifer seed crops, which develop seasonally in the late spring and early summer but on a highly unpredictable spatial pattern (Génard & Lescourret, 1987, Summers et al., 2002; Newton, 2006b). Conifer seed crops may also decline suddenly and unpredictably, making irruptive movements relatively common in conifer seed specialists (Benkman, 1993; Newton, 2006). Despite showing flexibility in the
timing, duration, and direction of migration compared to seasonal obligate migrants, red crossbills do show some seasonality with their migratory behaviors and physiology – probably because cone crop development is seasonally consistent (Newton, 1967; Berthold, 2001; Cornelius & Hahn, 2012; Cornelius et al., 2021). Fat deposits in both free-living and captive red crossbills peak in May and June, even when fed unlimited food on constant temperature and natural photoperiod in the lab (Cornelius & Hahn, 2012; Cornelius et al., 2021). The seasonal physiological preparations observed in captive crossbills, independent of food availability or changes in photoperiod cues, suggest that crossbill migrations may be more similar in nature to regular, seasonal migrations than previously appreciated. Here I utilize the predictable seasonal cycle of fat deposition and the flexible migratory behavior of red crossbills in a lab setting to explore how social and photoperiodic environmental cues impact the preparations for and the initiation of migration.
Experimental Design

Capture and Transfer to Captivity

Ninety-six red crossbills were captured using mist nets in the west Cascades of Oregon and Washington in September and October of 2019. Captured birds included adults (N = 30 male and 25 female) and winter-born juveniles (N = 22 male and 32 female) that had all previously experienced at least one migratory season prior to capture, and all were of the red crossbill eco-type 2—as identified by call structure (Groth, 1993). Type 2 red crossbills are large-billed and are specialists on the cones of the ponderosa pine (Pinus ponderosa), lodgepole pine (Pinus contorta), and some firs and spruces (Benkman & Young, 2019; Kelsey 2008). All birds were placed in group aviaries with ad libitum pellet food (Roudybush maintenance diet), stable room temperature, and photoperiod mimicking the natural photoperiod for Corvallis, Oregon, to acclimate to captivity before the beginning of the experiment.

Experimental Housing

Between February 12 and February 24 birds were moved from group aviaries into individual cages in three different experimental rooms. During this process, birds were assigned to one of five groups, three of which were focal treatment groups and two of which were social stimulus groups. Focal treatment groups included: alone control birds (AC; N = 12) that remained in visual isolation from other crossbills for the entirety of the experiment; social control birds (SC; N = 14) that were given neighbors in the same pre-migratory state; and social experimental birds (E; N = 14) that were given neighbors in an advanced migratory state. The stimulus birds were housed in pairs to be either photo-advanced into a migratory state for later pairing with group E (EN; N = 28), or to remain on natural photoperiod and serve as stimulus
birds for group SC (SCN; \( N = 28 \)). Ages and sexes were balanced across all groups. Focal birds were given neighbors of the same sex that had not previously been housed in the same group aviary. Previous studies have found that both sexes show similar migratory behavior (Cornelius & Hahn, 2012; Watts et al., 2017), but sexes were kept separate to reduce variation related to reproductive behavior or physiology. All birds were housed with opaque plastic dividers prior to pairing such that they could hear other birds in the room but could not see other birds.

**Photoperiod Treatment of Stimulus Birds**

On March 9th, two weeks after transfer to individual cages, stimulus birds in the EN group were photo-advanced to a daylength coincident with peak migratory behavior in wild and captive birds (i.e., Jun 1 daylength: 15.5 hours light, 8.5 hours dark; Cornelius & Hahn, 2012). EN birds remained on this photoperiod until pairing four weeks later.

**Social Stimulus**

Social stimuli were given to E and SC groups on April 10. This date was chosen because pre-migratory preparations start to become evident in captive crossbills in early May; thus, an early April pairing allowed for several weeks of social stimulus to advance pre-migratory preparations. All birds were moved to a new room on pair-day and were housed as follows (Figure 2): AC birds still had dividers in place between individuals, SC birds were housed next to an SCN stimulus pair without a divider, and E birds were housed next to an EN stimulus pair without a divider. Thus, all birds receiving social information had visual contact with one other cage. Each focal group was housed in a separate room; thus, AC birds could hear other AC birds, SC birds could hear SC and SCN birds, and E birds could hear E and EN birds. The migratory condition of all birds in the study was monitored once per week throughout the study using
measures of physiology described below, and behavior was monitored continuously throughout the study as described below.

**Figure 2**

*Diagram of the Experiment Groupings of the Birds*

![Diagram of Experiment Groupings of the Birds](image)

*Note.* (a) Represents the alone control group, a focal bird with no stimulus partners. (b) Represents the partner control group, a focal bird with stimulus birds of the same migratory life stage. (c) Represents the stimulation group, a focal bird with stimulus birds in a different migratory state.

**Body Condition**

Body condition metrics were scored by a single experienced observer. Fats deposits were quantified using a visual scoring system of the furcular and abdominal region on a scale from 0 (no visible fat) to 5 (bulging fat depositions) as described previously in songbirds (Helms & Drury, 1960) and in red crossbills (Hahn, 1998; Cornelius & Hahn, 2012). The two scores were
summed for analysis. Muscle hypertrophy was visually scored on a scale from 0 (emaciated, concave muscle) to 3 (convex muscle, bulging, obscures sternum; Bairlein, 1995). Mass was measured to the nearest 0.01 g using a bench-top electronic scale. Data were collected at the same time of day for each group (i.e., all physiology metrics were collected between 2 and 4 hours after lights-on) and all individuals of a group were sampled on the same day of the week.

**Behavioral expression**

Activity was measured continuously throughout the experiment using infrared activity monitors (Starr Life Sciences; Watts et al., 2017) for all focal birds (AC, SC, and E groups). For stimulus pairs (SCN and EN), dedicated activity monitors were rotated between two cages so that each pair had 3 or 4 days of continuous activity data recorded per week. Activity data were recorded by a computer as the sum of infrared beam-breaks per minute. Data were exported via Excel spreadsheets and were condensed using Program R to create binned totals of daily activity that were averaged for each bird for each week of the experiment. Activity data were also grouped into weekly averages of diurnal vs nocturnal daily activity. Diurnal activity was determined as starting the first hour in which lights were turned on and concluding with the hour that lights were turned off. Nocturnal activity was recorded in the hours in which there was complete darkness.

**Data Analysis**

Statistical analyses were performed with Program R v. 3.6.2 (R Core Team, 2019) and JMP (JMP®, Version 16.0. SAS Institute Inc., Cary, NC, 1989–2021). The condition metrics of body mass, fat and muscle score are often highly correlated in birds and are probably not independent (Balbontín et al., 2012) and all three scores are expected to increase during
premigratory preparations, thus these were collapsed into a single estimate of condition through principal component analysis. All three variables loaded positively onto the first principal component (PC1) and PC1 explained 54% of the variation (loadings were 0.69 for mass, 0.70 for fat, and 0.16 for muscle). PC1 was thus used in further analyses as a single metric of body condition.

Effects of photostimulation on Experimental Neighbor body condition were examined with a repeated measures ANOVA. Differences in mass between the weeks pre- and post-stimulation were further explored with matched pair analysis to determine which weeks differed. Effects of social pairing on both the body condition and activity of neighbor groups (EN and SCN) and focal groups (AC, SC, and E) were quantified with generalized linear mixed models using either a normal distribution (body condition; continuous variable) or a negative binomial distribution (activity; count variable). A continuous effect of experiment day, and categorical effects of treatment group, age, sex, and their interactions were included as fixed effects for the focal birds. Models describing the neighbor’s response to pairing did not include age given that neighbors were housed in pairs of mixed ages but same sex. Individual ID was included in all models as a random effect. Models were compared using a nested ANOVA to identify the model that best fit the data based on the lowest AIC. Parameter effects in each model were reported based on comparisons to the alone control group.
Results

Neighbor Responses to Photostimulation

Photostimulation caused an increase in mass in the experimental neighbors (EN) that was not observed in the social control neighbors (SCN; Repeated Measures ANOVA treatment*week \(F_{(3,51)} = 9.0437, p < 0.0001\); Figure 3). Photoadvanced experimental neighbors (EN) significantly increased mass immediately following photostimulation (Week 0 to Week 1, average change +1 g; matched pair analysis \(p = 0.0002\)), whereas social control neighbors (SCN) did not show any significant changes in mass (average change -0.1 g; matched pair analysis \(p = 0.72\)). There were no changes in activity during the first week following photostimulation in either EN or SCN groups (matched pair analyses \(p = 0.4\)). However, there was a significant interaction between treatment and date in a repeated-measures ANOVA for activity \((F_{(3,20)} = 5.9; p = 0.004)\) because the SCN increased activity levels between Weeks 1 and 2 (matched pair analysis; \(p = 0.0007\)), whereas EN slightly decreased in activity \((p = 0.05)\). Both groups increased activity between Weeks 2 and 3 (matched pair analyses; EN, \(p = 0.01\); SCN, \(p = 0.008\)).
Figure 3

*Graphical Representation of Mass Changes in Neighbor Birds Following Photostimulation*

Note. Experimental Neighbor birds showed a significant increase from week 0 to week 1 following photostimulation while Social Control Neighbors did not show any significant changes in mass in the 3 weeks following.

**Physiological Responses to Pairing During Pre-migratory Period**

**Focal Physiological Responses to Pairing**

The best model describing body condition of the focal birds included age and the interaction between experiment day and treatment group (Table 1). Juveniles were in lower condition relative to adults throughout the study (Age $\beta = -1.61; p = 0.02$), but model selection
did not identify an interaction of age with experiment day or treatment group as being important (Tables 1 and 2).

Table 1

*Model Selection Table for Body Condition of Focal Group*

<table>
<thead>
<tr>
<th>Models</th>
<th>Params</th>
<th>deltaAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Day * Treatment + Age</td>
<td>9</td>
<td>0.00</td>
<td>0.80</td>
</tr>
<tr>
<td>Experiment Day * Treatment + Sex</td>
<td>9</td>
<td>3.71</td>
<td>0.13</td>
</tr>
<tr>
<td>Experiment Day * Treatment</td>
<td>8</td>
<td>4.65</td>
<td>0.08</td>
</tr>
<tr>
<td>Experiment Day + Treatment</td>
<td>6</td>
<td>18.42</td>
<td>0.00</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>4</td>
<td>18.71</td>
<td>0.00</td>
</tr>
<tr>
<td>Experiment Day * Treatment * Age</td>
<td>14</td>
<td>19.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Experiment Day * Treatment * Sex</td>
<td>14</td>
<td>21.61</td>
<td>0.00</td>
</tr>
<tr>
<td>AIC of Top Model: 316.849</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Body condition did not differ between treatment groups (Tables 1 and 2; ANOVA $F_{(2,39)} = 1.0; \ p = 0.37$), but was affected by the interaction between treatment group and experiment day (Tables 1 and 2).

Table 2

*Model Summary of Top Supported Model Describing Body Condition From Table 1*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>df</th>
<th>t value</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.54</td>
<td>0.70</td>
<td>37.52</td>
<td>0.78</td>
<td>0.44</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>-0.04</td>
<td>0.01</td>
<td>77.00</td>
<td>-3.36</td>
<td>0.001</td>
</tr>
<tr>
<td>Social Control</td>
<td>0.27</td>
<td>0.81</td>
<td>38.12</td>
<td>0.33</td>
<td>0.74</td>
</tr>
<tr>
<td>Experimental</td>
<td>0.14</td>
<td>0.80</td>
<td>38.14</td>
<td>0.17</td>
<td>0.86</td>
</tr>
<tr>
<td>Juvenile</td>
<td>-1.62</td>
<td>0.64</td>
<td>36.00</td>
<td>-2.53</td>
<td>0.02</td>
</tr>
<tr>
<td>Experiment Day * Social Control</td>
<td>0.05</td>
<td>0.02</td>
<td>77.00</td>
<td>3.46</td>
<td>0.0009</td>
</tr>
<tr>
<td>Experiment Day * Experimental</td>
<td>0.09</td>
<td>0.02</td>
<td>77.00</td>
<td>6.17</td>
<td>&lt; 0.00001</td>
</tr>
</tbody>
</table>

The change in body condition after 21 days post-pairing was positive and steeper in both social groups compared to controls, which declined in condition over the same period (Table 2;
Figures 4 and 5; AC vs. SC, \( p = 0.0009 \); AC vs. E, \( p < 0.0001 \)). However, the slope was larger in experimental birds relative to social controls (Figures 4 and 5; SC vs. E, \( p = 0.016 \)).

**Figure 4**

*Changes in Body Condition of Focal Birds Following Pairing With Neighbor Birds*

*Note.* Thick lines represent the trend line for the group based on the top supported model while the thinner lines represent individuals.
Figure 5

*Beta Coefficients for Each Focal Group Body Condition*

Note. Error bars are 95% confidence intervals around each slope estimate. Point estimates that are not included in another estimates’ confidence intervals are significantly different.

**Neighbor Physiological Response to Pairing**

The best model describing body condition in neighbors in the three weeks following pairing included sex and the interaction between experiment day and treatment group (Table 3). Male neighbors had higher body condition than did females ($\beta = 1.9; p = 0.003$; Table 4), but this did not influence the interaction between experiment day and treatment group according to the model.
Table 3

Model Selection Table for Different Models Describing Body Condition in Neighbors

<table>
<thead>
<tr>
<th>Model</th>
<th>Params</th>
<th>deltaAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Day * Treatment + Sex</td>
<td>7</td>
<td>0.00</td>
<td>0.98</td>
</tr>
<tr>
<td>Experiment Day * Treatment</td>
<td>6</td>
<td>7.52</td>
<td>0.02</td>
</tr>
<tr>
<td>Experiment Day * Treatment * Sex</td>
<td>10</td>
<td>16.16</td>
<td>0.0003</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>4</td>
<td>23.15</td>
<td>0.00</td>
</tr>
<tr>
<td>AIC of Top Model: 470.2605</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4

Summary of Top Model Describing Body Condition in Neighbors

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>df</th>
<th>t value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.644</td>
<td>0.511</td>
<td>53.861</td>
<td>-3.218</td>
<td>0.002</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>0.017</td>
<td>0.009</td>
<td>106.000</td>
<td>1.788</td>
<td>0.077</td>
</tr>
<tr>
<td>Treatment Group</td>
<td>-1.054</td>
<td>0.614</td>
<td>55.016</td>
<td>-1.717</td>
<td>0.092</td>
</tr>
<tr>
<td>Male</td>
<td>1.867</td>
<td>0.606</td>
<td>51.000</td>
<td>3.081</td>
<td>0.003</td>
</tr>
<tr>
<td>Experiment Day * Treatment Group</td>
<td>0.070</td>
<td>0.013</td>
<td>106.000</td>
<td>5.323</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Experimental neighbors, which were photoadvanced prior to pairing, continued to show increases in body condition after pairing ($p < 0.0001$; Figure 6) while the social control neighbors had no overall change in body condition ($p = 0.147$; Figures 6 and 7).
Figure 6

*Changes in Body Condition of Neighbor Birds Following Pairing with Focal Birds*

*Note.* Thick lines represent the trend line for the group based on the top supported model while the thinner lines represent individuals.
Figure 7

*Beta Coefficients for Each Neighbor Group Body Condition*

![Graph showing beta coefficients for each neighbor group body condition.](image)

**Note.** Error bars are 95% confidence intervals around each slope estimate. Point estimates that are not included in another estimates’ confidence intervals are significantly different.

**Behavioral responses to pairing during the pre-migratory period**

*Focal Behavioral Response to Pairing*

Focal activity was most influenced by the three-way interaction between experiment day, treatment group, and age according to model selection (Tables 5 and 6).
Table 5

*Comparison of Models Describing Activity in Focal Birds Following Pairing*

<table>
<thead>
<tr>
<th>Model</th>
<th>Params</th>
<th>deltaAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Day * Treatment * Age</td>
<td>14</td>
<td>0.00</td>
<td>1</td>
</tr>
<tr>
<td>Experiment Day * Treatment * Sex</td>
<td>14</td>
<td>34.49</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>4</td>
<td>36.04</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day + Treatment</td>
<td>6</td>
<td>37.37</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day * Treatment</td>
<td>8</td>
<td>37.92</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day * Treatment + Age</td>
<td>9</td>
<td>39.83</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day * Treatment + Sex</td>
<td>9</td>
<td>39.97</td>
<td>0</td>
</tr>
<tr>
<td>AICc of Top Model: 12881.3362</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 6

*Model Summary of Top Model Describing Activity in Focal Birds Following Pairing*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z value</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>7.92</td>
<td>0.16</td>
<td>50.88</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>0.01</td>
<td>0.004</td>
<td>2.24</td>
<td>0.02</td>
</tr>
<tr>
<td>Experimental</td>
<td>0.03</td>
<td>0.20</td>
<td>0.13</td>
<td>0.90</td>
</tr>
<tr>
<td>Social Control</td>
<td>0.11</td>
<td>0.20</td>
<td>0.53</td>
<td>0.59</td>
</tr>
<tr>
<td>Juvenile</td>
<td>0.37</td>
<td>0.20</td>
<td>1.81</td>
<td>0.07</td>
</tr>
<tr>
<td>Experiment Day * Experimental</td>
<td>0.002</td>
<td>0.005</td>
<td>0.36</td>
<td>0.72</td>
</tr>
<tr>
<td>Experiment Day * Social Control</td>
<td>-0.003</td>
<td>0.005</td>
<td>-0.60</td>
<td>0.55</td>
</tr>
<tr>
<td>Experiment Day * Juvenile</td>
<td>-0.01</td>
<td>0.005</td>
<td>-1.92</td>
<td>0.05</td>
</tr>
<tr>
<td>Experimental * Juvenile</td>
<td>-0.18</td>
<td>0.28</td>
<td>-0.63</td>
<td>0.53</td>
</tr>
<tr>
<td>Social Control * Juvenile</td>
<td>-0.43</td>
<td>0.28</td>
<td>-1.53</td>
<td>0.13</td>
</tr>
<tr>
<td>Experiment Day * Experimental * Juvenile</td>
<td>-0.01</td>
<td>0.01</td>
<td>-1.59</td>
<td>0.11</td>
</tr>
<tr>
<td>Experiment Day * Social Control * Juvenile</td>
<td>-0.02</td>
<td>0.01</td>
<td>-2.53</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Adults in all treatment groups showed very modest increases in activity after pairing (Figure 8). Juvenile responses to pairing, however, differed by treatment group: E and SC juveniles both decreased in diurnal activity during the three weeks after pairing ($\beta = -0.01, p = 0.05; \beta = -0.02, p = 0.01$), whereas the alone control juveniles showed no change (Figure 9).
Individual variation within nocturnal activity levels were large; however there does not appear to be any group level changes in nocturnal activity levels.

**Figure 8**

*Changes in Daily Activity Levels for Focal Birds*

*Note.* The top graph shows the change in the group mean with standard error in adults (upper left) and juveniles (upper right). The bottom graphs show predicted values based on the top supported model with 95% confidence intervals for adults (bottom left) and juveniles (bottom right).
Figure 9

Beta Coefficients for Each Focal Group Activity Levels

*Note.* Error bars are 95% confidence intervals around each slope estimate. Point estimates that are not included in another estimates’ confidence intervals are significantly different.

Neighbor Behavioral Responses to Pairing

Model selection suggests the interaction between experiment day, treatment group, and sex is important in describing activity levels of the neighbor birds (Tables 7 and 8).
Table 7

Model Selection Comparing Different Models Describing Activity in Neighbors Following Pairing

<table>
<thead>
<tr>
<th>Model</th>
<th>Params</th>
<th>deltaAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment Day * Treatment Group * Sex</td>
<td>12</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Experiment Day * Treatment Group + Sex</td>
<td>9</td>
<td>22.7595</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day * Treatment Group</td>
<td>8</td>
<td>23.9948</td>
<td>0</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>6</td>
<td>27.6724</td>
<td>0</td>
</tr>
<tr>
<td>AICc of Top Model – 6058.9505</td>
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<td></td>
<td></td>
</tr>
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</table>

Table 8

Summary of Top Supported Model from Table 7

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>SE</th>
<th>z value</th>
<th>P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>7.30</td>
<td>0.11</td>
<td>64.68</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Experiment Day</td>
<td>0.01</td>
<td>0.003</td>
<td>2.68</td>
<td>0.01</td>
</tr>
<tr>
<td>Experimental Neighbor</td>
<td>0.30</td>
<td>0.15</td>
<td>2.03</td>
<td>0.04</td>
</tr>
<tr>
<td>Male</td>
<td>0.27</td>
<td>0.15</td>
<td>1.72</td>
<td>0.09</td>
</tr>
<tr>
<td>14 Hours</td>
<td>0.87</td>
<td>0.04</td>
<td>20.15</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>24 Hours</td>
<td>1.18</td>
<td>0.04</td>
<td>30.96</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Experiment Day * Experimental Neighbor</td>
<td>-0.01</td>
<td>0.005</td>
<td>-2.64</td>
<td>0.01</td>
</tr>
<tr>
<td>Experiment Day * Male</td>
<td>-0.02</td>
<td>0.005</td>
<td>-3.55</td>
<td>0.0004</td>
</tr>
<tr>
<td>Experimental Neighbor * Male</td>
<td>-0.17</td>
<td>0.22</td>
<td>-0.81</td>
<td>0.42</td>
</tr>
<tr>
<td>Experiment Day * Experimental Neighbor * Male</td>
<td>0.03</td>
<td>0.01</td>
<td>5.36</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

Experimental neighbor males and social control females increased activity following pairing with focal birds ($p < 0.00001; p = 0.03$; Figures 10 and 11), whereas experimental neighbor females and social control males did not ($p = 0.7; p = 0.07$; Figures 10 and 11).
Figure 10

*Changes in Daily Activity Levels for Neighbor Birds Following Pairing*

*Note.* Trend lines are generated from the top supported model with 95% confidence intervals.
Figure 11

*Beta Coefficients for Each Neighbor Group Daily Activity*

![Graph showing beta coefficients for different groups.](image)

**Note.** Error bars are 95% confidence intervals around each slope estimate. Point estimates that are not included in another estimates’ confidence intervals are significantly different.
Red crossbills in this study appeared to use social cues from conspecifics to initiate or fine-tune seasonal migratory preparations. Experimental birds showed a small but highly consistent increase in body condition after being paired with photo-advanced neighbors that was similar in degree to the changes in mass observed during the migratory period in wild crossbills (Cornelius et al., 2021). The social control group --- on the other hand --- showed no change in body condition after pairing – suggesting that the migratory state of the neighbor was important in inducing the observed effect. The alone control group, which also experienced a move to a new room but was not paired with a neighbor, declined in body condition --- suggesting a negative impact of social isolation on body condition when environmental conditions are variable. These results thus support the hypothesis that social cues can accelerate migratory preparations in this nomadic species. Behavioral changes in activity, on the other hand, did not differ between social treatment groups and were age-dependent. This difference between the physiological and behavioral responses to pairing suggests that the two processes are likely regulated by separate pathways.

An apparent independence of the mechanisms controlling pre-migratory preparation and migratory behavior may be unique to species with more facultative migratory behavior, but has also been detected in regular seasonal migrants. For example, in white-crowned sparrows (Zonotrichia leucophrys), small variations in light levels can induce nocturnal restlessness without inducing the hyperphagia that is typical of the pre-migratory phenotype (Ramenofsky et al., 2008). The onset of migratory behavior in birds is normally induced by a mix of cues involving photoperiod, endogenous state (i.e., fuel reserves) and environmental conditions (King & Farner, 1959; Ramenofsky & Wingfield, 2007; Bauer et al., 2011). Crossbills are nomadic and
field observations suggest that they regularly move to find newly developing cone crops in late spring and early summer, but their movements are also clearly impacted by conifer seed crop size and intraspecific competition for those seeds (Koenig & Knops, 2001; Cornelius, unpublished data). Migrant birds that make seasonal movements use photoperiod and endogenous rhythms to time their preparations and some studies suggest that nomadic species may do the same if migratory movements are temporally consistent (Cornelius et al., 2012; Watts et al., 2017; Cornelius et al., 2021; Berthold, 1977). The change in pre-migratory condition that occurred in this study when experimental neighbors were photo-advanced supports this assertion and suggests that physiological preparation for movement may consistently occur in crossbills, even if the actual decision to depart is more facultative. Seasonal preparation in this nomadic species thus appears to be similar to that of seasonal migrants --- where photoperiod induces pre-migratory fat gain --- but may also be sensitive to other types of environmental cues like social information. While facultative migrants and obligate migrants may both be using social or supplementary cues to fine-tune migration, obligate migrants are likely utilizing these cues to a lesser degree given that facultative migrants have greater variability in when and where they migrate and decisions can be more closely related to what conditions are like locally, rather than at a destination (Ramenofsky et al., 2012).

Adequate fat stores are required by migratory birds to successfully complete their migratory journeys (King & Farner, 1959; Odum, 1960). The actual size of these fat stores can vary greatly because there is a trade-off between the energy provided by the extra fat stores and the associated costs of carrying the extra mass during the migratory flight (Klaassen, 1996). Premigratory fat deposits in facultative migrants are predicted to be smaller than for most obligate migrants (Alerstam & Lindstrom, 1990), and a recent comparative study of four facultative
migrant species, including red crossbills, supports that prediction (Cornelius et al., 2021). Red crossbills occur as a suite of different eco-types that vary in their morphology based on their preferred conifer food source (Benkman, 1993) — with 10 eco-types currently described in North America (Groth, 1993). While many of the eco-types appear to show similar seasonality in regards to migration and breeding schedules, there is support for the notion that the differences in temporal patterns of their preferred conifer food source may impact the behaviors associated with their seasonality (Fowells, 1968; Hahn, 1998; Koenig & Knops, 2000; Cornelius et al., 2021). Most published data on crossbills comes from the type 3 eco-type, which feed of the seeds of hemlock (*Tsuga* spp.) and spruce (*Picea* spp.). These species of conifer tend to produce seed in boom-and-bust cycles and therefore type 3 crossbills may need to cope with higher variability in food when compared to the other eco-types. Type 2 crossbills on the other hand, the type used in this experiment, rely primarily on pine species as their main food source (Groth, 1993; Kelsey, 2008). Some pine species may provide a more reliable food source and the migratory range may be smaller for type 2 crossbills compared to type 3 (Benkman & Young, 2020; Cornelius et al., 2021); thus, preparations for migration or breeding could be expected to differ between them.

The type 2 red crossbills in this study showed a small but consistent increase in body condition (i.e., 4% increase in body mass) over the course of the experiment. This increase is consistent with the fat increases observed in wild Type 2 crossbills during the migratory season (Cornelius et al., 2021). Migratory birds are expected to have lower wing loading as means of reducing flight costs and migrants that travel longer distances tend to have longer wings to maintain lower wing loading (Norberg, 1985; Bowlin & Wikelski, 2008). Type 2 crossbills have higher wing loading than type 3 crossbills (Cornelius et al., 2021), further suggesting that type 2 crossbills make less frequent or shorter migratory trips. Shorter migrations should require less fuel (Vincze
et al., 2019), thus the small but consistent increases in body condition observed in type 2 red crossbills in this experiment appear to match their anticipated migratory needs.

An increase in activity levels can be a sign of migratory initiation in many captive migratory birds (Helm & Gwinner, 2006, Eikenaar et al., 2014). The birds that have been most studied in this regard are nocturnal migrants and while diurnal migrants may also exhibit changes in activity levels related to migration, these changes may be more difficult to detect (Alerstam & Ulfstrand, 1975; Munro & Munro, 1998). With migratory restlessness, increases in nighttime activity can be seen as a sign of restlessness because the activity is outside of the norm for the time of day. Diurnal migrants, however, may display an increase in daytime activity that is masked or made difficult to interpret by the routine activity of the bird. Migratory behavior in this experiment, as measured by activity, was age and treatment specific. The activity levels of the experimental, social control, and alone control adult focal birds did not appear to differ in any significant way in this study—all groups of adults showed a trend for activity to increase over the course of the experiment, but Experimental adults were the only birds with a slope that was significantly different from zero. Juveniles in the experimental and social control groups, however, differed significantly from their adult counterparts with both groups showing a significant decrease in activity after pairing. The juveniles of the alone control group showed no significant change in activity–similar to the alone control adults. It is possible that the decrease in activity observed in juveniles of the two social groups indicates a form of settlement behavior due to their paring with adult birds. This may also explain why there was no observable difference in the adults and juveniles of the alone control group because the juveniles never received social cues from a neighboring bird.
Adult and juvenile individuals of the same species may experience and respond to their physical and social environment in differing manners (Holland & Helm, 2013; Acampora et al., 2014; Rotics et al., 2016; Breen et al., 2020). Hypotheses regarding migration and age include the following: (a) juvenile birds may simply be more plastic and sensitive to environmental cues, resulting in different or more extreme responses, (b) juveniles may rely on endogenous or genetic programs more than their adult counterparts, or (c) adults that have experienced more migrations may alter sensitivity to environmental and social cues. These differing experiences may help to explain the differences observed in the migratory behavior of our adult and juvenile birds.

Juvenile individuals within a migratory species often face higher mortality during their first few migrations compared to experienced adults (Rotics et al., 2016). In migratory gull species, juveniles are observed to occupy a wider variety of overwintering habitats when compared to adults because they are excluded from the most optimal habitats (Kilpi & Saurola, 1984). Differences in experience between juvenile and adult migratory birds can often mean that the juveniles are relying on the adults for cues and information about migration. Juvenile white storks rely on migratory adults for navigational purposes and will even leave stopover sites before properly refueling to avoid being left behind by the social group (Rotics et al., 2016). Individuals separated from the group sometimes fail to complete their winter migrations (Rotics et al., 2016). In Palearctic vulture species, high mortality among migrating juveniles is hypothesized to be due to an increasing decline in experienced adult birds (Oppel et al., 2015). Without conspecifics for the juveniles to learn from, the birds may use less than optimal migratory routes which leads to increased mortality (Oppel et al., 2015). These cues from more experienced adults are likely most important in species with higher degrees of variation in their
migratory behavior or patterns, whereas more obligate migratory species may rely more heavily on internal cues. Endogenous cues are the standard for many passerine migratory species with these cues aiding in the timing, direction, and location of migrations (Helbig, 1991; Gwinner, 1996; Åkesson et al., 2014). Naïve or juvenile individuals of an obligate migratory species may use endogenous cues to process space, compass, timing, and route information related to the population level migratory pattern (Helbig, 1991; Gwinner, 1996; Åkesson et al., 2014) and as a result social cues from more experienced individuals become less important. It remains to be seen if the social cue effects on migratory timing demonstrated in this study with facultative migrants extends to the broader group of obligate, seasonal migrants as well.

The alone control focal birds in this study faced the unique challenge of being visually isolated from one another. Visual isolation from conspecifics can also be a significant source of stress for individuals. Visual isolation is known to initiate a peeping response in young pigeons when they are in an unfamiliar environment (de Souza et al., 2009) and visual isolation affects singing behavior in first-year zebra finches (Zann & Dunn, 1997). The alone controls were able to hear other individuals in the room but were completely visually isolated, thus it is possible that the visual isolation experienced by the alone control birds resulted in depressive psychological effects possibly driving the decline in body condition. Strong correlations between isolation and increased depressive symptoms have been observed in humans. Depression in humans is linked to a U-shaped distribution of weight (i.e. severely underweight or severely overweight; de Wit et al., 2009) while anxiety has also been linked to either significantly higher or lower BMI scores in both men and women (Zhao et al., 2009). I observed a slight decline in body condition in the alone control birds over the course of the experiment and body mass and fat scores were generally lower than those observed in socially housed birds. These differences may be related to
anxiety and depression-like symptoms in the isolated birds. Stressors have been shown to decrease the food intake and overall size of individuals in birds raised for the meat industry (Ferket & Gernat, 2006). These stressors often present themselves as environmental or immunological and do not simply decrease food intake but negatively affect nutrient absorption and gut motility (Ferket & Gernat, 2006). There were no significant changes in food intake in the alone control birds, so the declining body condition observed over the course of the experiment may have been related to the stress caused by social isolation. These patterns observed in the alone control birds provides additional support for the importance of social cues in the lives of the red crossbill.

In conclusion, social cues appear to be important in facultative nomadic songbirds like the red crossbill. Socially isolated birds declined in condition over time whereas socially housed birds increased condition dependent on the migratory status of their neighbors. This suggests that social cues are an important aspect of the red crossbills physical and social environment and that these cues are even more important for migratory or pre-migratory individuals. This work has aimed to fill in some of the knowledge gaps in the literature regarding non-photoperiodic timing mechanisms in migrants and expands our understanding of facultative migratory behavior. Such mechanisms may promote flexibility and resource matching in migrants if resources shift relative to photoperiod and, thus, could prove important in species adaptive capacity to changing resources.
References


