

ENVIRONMENTAL CONDITIONS AFFECT THE BEHAVIOR OF CAPTIVE, MIGRATORY WHITE-CROWNED SPARROWS

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Abstract. Many aspects of migration have been studied extensively, but little is known of how environmental conditions influence the behaviors displayed by migrants. Field studies suggest that such environmental factors as atmospheric conditions, nocturnal illumination, and food availability can affect migratory activity. We used 24 hr locomotor activity records and specific behaviors displayed by captive migrants to determine how nocturnal illumination and food restriction altered the migratory behavior of Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*). Our results indicated that nocturnal locomotor activity was enhanced with increased nocturnal illumination at the source from 0 to 9 lux, even though the intensity of illumination that reached the birds remained <1 lux. Food deprivation had little effect on migratory restlessness per se, but resulted in increased locomotor activity during daylight hours and behaviors associated with attempts to escape from the cage. Thus, we suggest that migrants respond to variations in environmental conditions by altering both day and nighttime behaviors. Plasticity of behavior would allow free-living migrants to respond quickly to changes in the environment, thus enhancing the likelihood of successfully reaching their destinations.

Key words: *beak-up flight, food restriction, Gambel's White-crowned Sparrow, locomotor activity, migratory restlessness, moonlight, Zonotrichia leucophrys gambelii.*

Efecto de las Condiciones Ambientales en el Comportamiento en Cautiverio de la Especie Migratoria *Zonotrichia leucophrys*

Resumen. Varios aspectos de la migración han sido intensamente estudiados, pero se sabe poco acerca de cómo las condiciones ambientales influyen el comportamiento de las aves migratorias. Los estudios de campo sugieren que factores ambientales como las condiciones atmosféricas, la iluminación nocturna y la disponibilidad de alimento pueden afectar la actividad migratoria. En este estudio usamos registros de actividad locomotora durante 24 horas y los comportamientos específicos observados en aves migratorias en cautiverio, para determinar cómo la iluminación nocturna y la restricción alimenticia alteran el comportamiento migratorio de *Zonotrichia leucophrys gambelii*. Nuestros resultados indicaron que la actividad motora nocturna aumentó con el incremento de la iluminación nocturna en la fuente de 0 a 9 lux a pesar de que la intensidad de la iluminación que las aves recibieron fue menor de 1 lux. La privación de alimento tuvo poco efecto en la intranquilidad migratoria de las aves per se, pero resultó en un incremento en la actividad locomotora durante el día y en el comportamiento asociado con intentos de escapar de las jaulas. De esta manera, nuestro estudio sugiere que las aves migratorias responden a variaciones en las condiciones ambientales alterando tanto su comportamiento diurno como nocturno. La plasticidad en el comportamiento permitiría a las aves migratorias responder rápidamente a los cambios ambientales en condiciones silvestres, aumentando así las posibilidades de llegar exitosamente a sus destinos.

INTRODUCTION

Migration is the annual movement to breeding grounds in spring (vernal stage) and wintering sites in fall (autumnal stage). Both stages can be divided into three distinct phases (Jacobs and Wingfield 2000, Ramenofsky and Wingfield 2007). First, the "development" phase starts with the increase in daylength (photoperiod; Farner 1955, Schwabl and Farner 1989) or endogenous circannual rhythms (Gwinner 1986, Berthold 2003, Gwinner and Helm 2003) or a combination

of both (Wingfield et al. 1990). Biochemical and physiological processes begin and culminate with the achievement of the second phase, "migratory disposition" or "mature capability," in which the behavior and physiology associated with flight and fueling are expressed (Jacobs and Wingfield 2000, Ramenofsky and Wingfield 2006). Once birds enter the mature capability phase, variations in behavior and physiology appear to be influenced by a variety of factors. For example, field observations note that the timing of departure for migratory movement occurs under atmospheric and climatic conditions that are conducive

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to flight, including clear skies, advantageous tail winds, and the full phase of the moon (Elkins 1983, Richardson 1990, Cochran and Wikelski 2005). Orientation can be influenced by low-intensity light, the earth's magnetic field, and solar and star compasses (Able 1993, Åkesson et al. 1996, Wiltshko and Wiltshko 2003, Cochran et al. 2004). Availability of food at stopover sites and energetic condition also affect migratory activity in captive and free-living birds (Gwinner et al. 1988, Loria and Moore 1990, Yong and Moore 1993, Newton 2006, Hitch and Leberg 2007). Alterations in the landscape, pollution, storms, and global climate change contribute to changes in migratory routes as well as locations of stopover and breeding sites of various migratory species (Coppack and Both 2002, Both et al. 2005, Hüppop and Winkel 2006). Timing of departure from stopover sites of some migrant species may also be influenced by social interactions (Lank 1985, Piersma et al. 1990). Once the destination is reached, factors that regulate the final or "termination" phase of migration are largely unknown, but a number of studies have suggested that environmental conditions play an instrumental role (Hahn et al. 1995, Wingfield et al. 2004, Ramenofsky and Wingfield 2006).

Previous studies have described daily patterns of behavior and plasma hormones in captive Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) during the mature capability phase of both the autumnal and vernal migratory stages (Ramenofsky et al. 2003, Landys et al. 2004, Agatsuma and Ramenofsky 2006). The behaviors and timing of their expression provide critical information about the activities of free-living counterparts that are difficult to follow in highly mobile species. We therefore used captive birds to investigate how external conditions affect behavior and the underlying mechanisms by which free-living migrants respond to alterations in the environment. The results of captive studies can offer useful information about the intricate interactions of migrants with the environment and provide valuable clues as to how individuals may respond to the rapid ecological changes currently taking place on a global scale.

We hypothesized that migrants in the mature capability phase (ready and able to migrate) would rely on environmental cues to regulate their daily behaviors. To test this hypothesis, we focused on two factors that could influence the behavior of migratory captive White-crowned Sparrows during both the autumnal and vernal migratory stages: (1) intensity of nocturnal illumination ("moonlight"), and (2) food availability. We predicted that increased intensity of "moonlight" would increase nocturnal locomotor activity and that food restriction would increase migratory restlessness.

METHODS

CAPTURE AND HOUSING

The Gambel's White-crowned Sparrow, a long-distance migrant that covers habitable terrain in successive short flights or bouts, breeds from the Canada-U.S. border into the arctic tundra and

taiga habitats of North America and overwinters in areas extending from the southwestern United States into northwestern Mexico (Blanchard and Erickson 1949, Cortopassi and Mewaldt 1965). During autumn migration in September 1999 and 2000, as birds passed through central Washington State, they were captured with mist nets at the Sunnyside Game Refuge (46°11'N, 119°54'W). Following capture, birds were transported to the Department of Biology at the University of Washington, Seattle, and held for one week in outdoor aviaries where they were exposed to natural photoperiods and temperatures.

From the outdoor aviaries, 20 birds (mixed age and sex classes) were selected at random and placed in individual cages (measuring 39 × 34 × 42 cm) in one of two environmental chambers (of dimensions 3.0 × 1.8 × 2.4 m) and allowed to acclimate to captive conditions for two weeks. The relative humidity of both chambers was held at 50%. Each chamber was equipped with fluorescent lighting with a measured output of 2300 lux at the source and 550 lux at the nearest cages by day. For nocturnal illumination, the chambers were fitted with a low-intensity nightlight (115 V or 0.03 W, LIMELITE™ Model 11100, Austin Innovations, Austin, Texas) placed centrally on the wall above the cages. While the intensity of light emitted at the source was measured at 6.45 lux, light intensity recorded at the cages positioned nearest to the nightlight was <1 lux.

Within each chamber, six birds were held in registration cages equipped for recording 24 hr locomotor activity while the other four were held in standard cages and used for measuring morphology, food consumption, and behavior. Food (Mazuri Chow, Nutrition International, Brentwood, Missouri, and mixed seeds, UW Custom Mix, Seed Factory NW, Inc., Kent, Washington) was available ad libitum except during a period of restriction. Water was always available and grit fortified with vitamins and minerals was provided weekly (Bird Health Grit, Seed Factory, Ceres, California).

PHOTOPERIOD MANIPULATIONS FOR AUTUMNAL AND VERNAL STUDIES

Two environmental chambers were employed in all studies, one serving as the control for the other. From the time of capture, natural daylength continued to shorten until the winter solstice. A midwinter photoperiod of 8 L:16 D (light:dark with lights off at 17:00) was used for the autumn studies, to unify the length of the recording and observation periods during this stage. Temperatures in the chambers ranged between 10° and 20°C daily, with the minimum at 01:00 and the maximum at 13:00. Under these conditions, birds exhibited nocturnal activity indicative of the autumnal migratory stage. Behavioral studies were conducted from October to mid-November. By December, nocturnal activity ceased as birds entered the winter stage (Landys et al. 2004, Agatsuma and Ramenofsky 2006).

In February, the same birds were exposed to a photoperiod of 18 L:6 D (lights off at 17:00), which reproduced a mid-breeding period daylength, again to achieve uniformity for

the length of the recording and observational periods. This photoperiodic manipulation induced hyperphagia, as birds increased body mass and fat deposition and exhibited migratory restlessness characteristic of the vernal migratory stage (Farner et al. 1961, Agatsuma and Ramenofsky 2006). Temperatures ranged from 10° to 20°C, with the minimum at 20:00 and the maximum at 08:00.

RECORDING LOCOMOTOR ACTIVITY

Each registration cage was equipped with a photodetector (Alarm Entry Device, RadioShack Corporation, Fort Worth, Texas) that emitted an infrared beam 0–10 cm above a central perch positioned 34 cm above the bottom of the cage. As birds passed through the beam, an electric signal was transmitted to a Macintosh computer. Locomotor activity was recorded and analyzed with a Labview computer program (National Instruments Corporation, Austin, Texas) that was further refined by “Perch Hopping Software” written by D. Baldwin (National Marine Fisheries Service, Seattle, Washington). The program collected signals and computed the average movement of each bird across the electronic beam per min over a 30 min interval for a total of 24 hr; this is referred to as locomotor activity and was previously described by Agatsuma and Ramenofsky (2006). Locomotor activity differed between the two stages. Thus, the daily records for the autumnal and vernal stages were divided into three periods: Afternoon (12:30–17:00), Night (autumnal = 17:00–09:00, vernal = 17:00–23:00), and Morning (autumnal = 09:00–12:00, vernal = 23:00–09:00; Fig. 1).

MONITORING BEHAVIOR

The locomotor records revealed daily patterns of activity over the 24 hr cycle and identified transitions between light and dark phases of the photocycle. To describe specific behaviors displayed by subjects and their locations within the cage, we chose four 2 hr observation sessions within each 24 hr period for videotaping: Session 1 (late afternoon) included the 2 hr preceding lights out (15:00–17:00), Session 2 (early night) encompassed the 2 hr following lights out (17:00–19:00), Session 3 (late night) was the 2 hr preceding lights on (07:00–09:00 in the autumnal and 21:00–23:00 in the vernal stage), and Session 4 (morning) consisted of the 2 hr following lights on (09:00–11:00 in the autumnal and 23:00–01:00 in the vernal stage; Fig. 1). Focal birds were filmed simultaneously during these sessions using Sony Video HI 8 XR CCD-TRV87 Handycams with infrared features.

In brief, behavior and identified locations of each bird within its cage were tabulated for the focal subjects from the videotapes using an instantaneous scan with 20 sec intervals per 10 min session, resulting in 30 total counts (Martin and Bateson 1993). We assigned the 10 min sessions to intervals of 10, 30, and 50 min after the beginning of each hour during the 4 hr tapes. Behavior and location data for

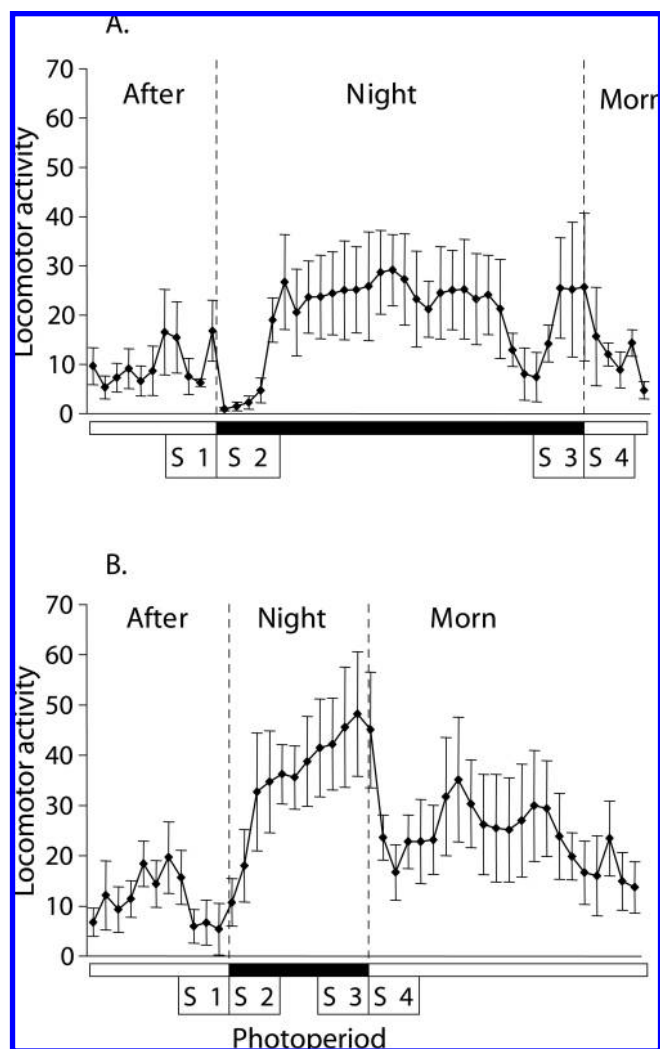


FIGURE 1. Comparative examples of 24 hr locomotor profiles (average movement across an electronic beam min^{-1} 30 min^{-1} interval) recorded from captive White-crowned Sparrows ($n = 6$) in the: (A) autumnal, and (B) vernal migratory stages. Daily divisions of Afternoon (After), Night, and Morning (Morn) represent periods into which the 24 hr records were divided and highlight the distinctions between day and night activity. The unfilled horizontal bar below the x axis indicates the light phase and the filled bar is the dark phase of each photoperiod. Sessions (S) 1 through 4 represent the four 2 hr divisions during which focal subjects were videotaped for behavioral observations: S 1 = late afternoon, S 2 = early night, S 3 = late night, S 4 = morning.

each bird were summed per hour, corrected for the total number of 10 min sessions observed, then averaged over each period, resulting in an average count per hour per period. A total of 158 hr of recorded behavior was analyzed for all the studies. Interobserver reliability of behavioral observations was tested by Pearson product moment correlation of observations made by two independent investigators of two separate 10 min video clips each with two focal birds ($r_{31} = 0.89$, $F = 113.2$, $P < 0.001$; Martin and Bateson 1993).

DESCRIPTIONS OF BEHAVIOR AND LOCATIONS IN CAGE

The day and nighttime behaviors observed included: rest (subject sits with little or no movement but may preen), jump (movement propelled by feet and legs), fly (movement propelled by wings), beak-up (bill pointed nearly vertically without wing beats, may move laterally on perch), beak-up flight (bill pointed nearly vertically with full wing beats at a frequency of 3–4 Hz, may lift off perch), and feed (searches for food and water). The beak-up and beak-up flight behaviors occurred during the dark phase and were characteristic of migratory restlessness. In both the autumnal and vernal stages, a period of quiescence was observed prior to the onset of migratory restlessness (Agatsuma and Ramenofsky 2006). As described earlier, birds sat motionless with their bellies pressed to or drooped over the perch. Some individuals appeared to sleep with the head tucked beneath one wing, while others maintained the head in the normal position. To determine the spatial use of cages, locations of the focal subjects were recorded during behavioral observations and included: above perch (subject in the air or moving to the side of the cage in the upper quadrant of the cage), perch (on perch), below perch (locations of food and water dishes), and floor (floor of cage). Exemplars of the behaviors recorded in the study may be viewed at <<http://faculty.washington.edu/mramenof/movies/Daytimebehave.html>> and <<http://faculty.washington.edu/mramenof/movies/Nightbehave.html>>.

MEASURES OF FOOD INTAKE AND MORPHOLOGY

Throughout the study, daily food intake was measured to the nearest 0.1 g on a Sartorius top-loading balance (VWR, West Chester, Pennsylvania). Food was delivered in covered dishes to reduce spillage and increase recording accuracy. Each day at 11:00, cages were inspected and any seeds and hulls spilled from the dishes were recovered. All hulls were removed from the cage and dishes and all remaining seeds and hulls were weighed. For each bird, daily food intake was calculated from the amount of food delivered the previous day minus that which remained 24 hr later. Cage bottoms were thoroughly cleaned, relined with fresh paper, and returned to the cage. Dishes were refilled with food and replaced in the cages. Immediately prior to food delivery on prescribed days, body mass was recorded to the nearest 0.1 g and fat score was visually estimated as a mean of the amount of fat deposited in the abdominal and chorio-clavicular areas on a scale from 0 (no fat present) to 5 (obese; Ramenofsky et al. 1999, 2003, Landys et al. 2004).

EXPERIMENTS

Moonlight studies. Nocturnal illumination was manipulated by either reducing or enhancing the amount of light emitted from the nightlight. Altering the intensity of the light source was achieved by the following: (1) unplugging the nightlight from the electrical socket but leaving it in place, resulting in

measurements of 0 lux at the source, (2) covering half of the lighted surface of one nightlight with opaque tape, giving 3 lux at the source and <1 lux at the cages nearest the light, (3) using one nightlight emitting 6.45 lux at the source and providing <1 lux at the nearest cages, and (4) using two nightlights, which resulted in 9 lux adjacent to the sources and <1 lux at the nearest cages. None of these levels of illumination produced sufficient amounts of light intensity to photostimulate the short-day birds.

Experiments were conducted during both the autumnal and vernal stages. Each test was run over a 48 hr period and locomotor activity was recorded continuously throughout. On Day 1, both chambers were exposed to one nightlight; the next night, the experimental chamber was given one of the four possible nightlight treatments, while the control chamber continued to be exposed to the one nightlight condition. After the conclusion of each test, both experimental and control chambers were exposed to one nightlight at night for at least two consecutive nights. Next, conditions were reversed, and the former control chamber was exposed to the test illumination and the second chamber served as its control with one nightlight. A balanced design was used for all experimental conditions of 0, 0.5, one, and two nightlights. Total locomotor activity recorded during the night under the specific lighting condition was used for analysis. It is possible that order of exposure to the experimental conditions or “round” may have influenced the results. The effect of round was tested by comparing total nocturnal locomotor activity of controls measured at each illumination for autumnal and vernal stages using a repeated measures MANOVA, with light intensity at the source, round, and season as variables. Results from these analyses revealed no effect of the three variables and no interactions across variables (all $F_{1,20} \leq 0.7$, all $P \geq 0.38$).

Food restriction studies. Experiments were conducted during the autumnal and vernal stages and were run over four days. Starting at 11:00 on Day 1 (fed condition), all birds (experimental and control) were provided with a measured amount of food, following which locomotor records were compiled for the three periods and observations were made for the four behavioral sessions. Measures of body mass, fat score, and 24 hr food consumption were recorded the following morning by 11:00. Starting on Day 2 (restricted condition), clean and empty food dishes were returned to the experimental birds, while those containing measured amounts of food were supplied to the controls. Locomotor records were collected and behavioral observations were conducted as previously described for Day 1. Body mass and fat scores were recorded for all birds and food consumption was measured only for controls the following morning at 11:00. Starting on Day 3 (fed condition), food was replaced for both groups and locomotor activity and behavioral data recorded. Body mass, fat scores, and food consumption were measured for all birds by 11:00 on Day 4.

STATISTICAL ANALYSES

Within each group and across control and experimental subjects, comparisons were made over the three locomotor activity periods or the four observational sessions. All data were tested for normality and equality of variances using Shapiro-Wilk W and Levene's tests. Nonparametric data were corrected using either Log_{10} or ArcTangent to give a normal distribution. When transformed distributions failed to meet the criterion for normality, nonparametric tests for repeated measures (Wilcoxon Sign Rank, Kolmogorov-Smirnov, or Friedman's test) or for comparing across groups (Wilcoxon test) were employed. Otherwise, a paired or unpaired t -test and two-way repeated measures MANOVA were used with variables of day and treatment. Post-hoc analyses were completed with Tukey's HSD or t tests and, where necessary, Bonferroni-adjusted P -values were used. Only two-tailed tests with significance set at $P < 0.05$ were used throughout. JMP 6.0 (SAS Institute, Inc., Cary, North Carolina) and SPSS 11.0 (SPSS, Inc., Chicago) statistical software was employed for analyses. All values reported in the results are means $\pm$ SE, except for behavioral data, which are medians $\pm$ 25th, 75th quartiles.

RESULTS

MORPHOLOGY AND FOOD INTAKE

Measures of body mass and food intake were similar in both migratory stages ($t_6 = -2.0$, $P = 0.1$; $z = -1.0$, $P = 0.3$, respectively; Table 1). However, birds in the vernal stage had greater deposits of subcutaneous fat ($z = -2.4$, $P < 0.02$), and birds in the autumn study ingested food at a faster rate than those in the vernal stage ($z = -2.4$, $P < 0.02$).

LOCOMOTOR ACTIVITY:

AUTUMNAL AND VERNAL STAGES

Locomotor activity records from birds in the autumnal and vernal stages revealed lower-level activity during daylight hours (afternoon and morning) and elevated nocturnal activity (Fig. 1). Prior to the onset of nocturnal activity in both stages, birds entered the quiescent phase, the timing of which differed. In autumn, quiescence occurred during the early night but in spring it preceded lights off (Agatsuma and Ramenofsky 2006).

MOONLIGHT: AUTUMNAL AND VERNAL STAGES

Increasing the intensity of light at the source during the night resulted in greater frequencies of nocturnal locomotor activity

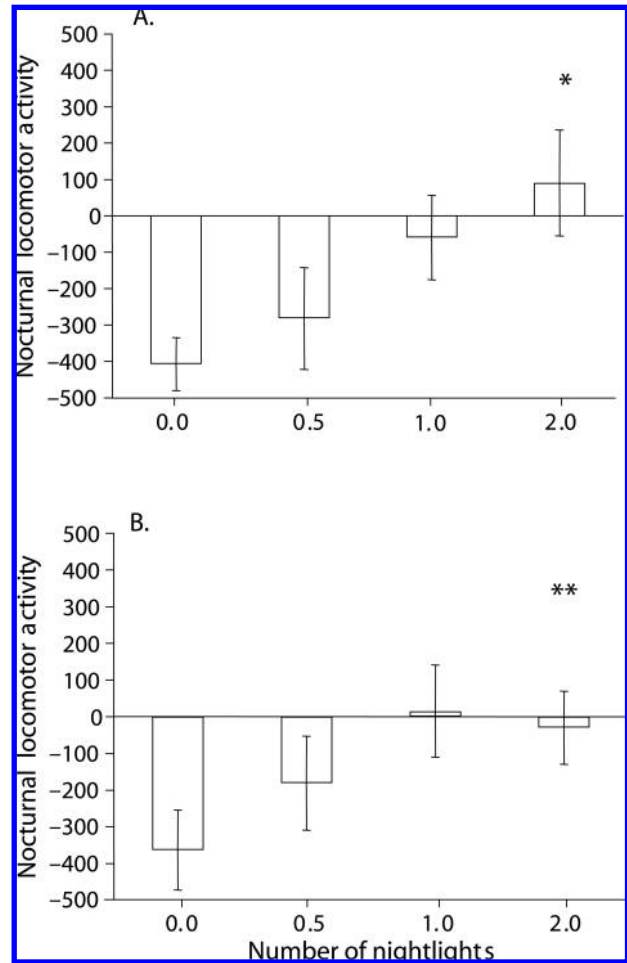


FIGURE 2. Nocturnal locomotor activity increased with enhanced low-level illumination in captive White-crowned Sparrows in both the: (A) autumnal, and (B) vernal migratory stages. Nocturnal locomotor activity, a measure of the average movement across an electronic beam min^{-1} 30 min^{-1} interval during the night phase, represents the difference between experimental birds exposed to one of four low-intensity nightlight treatments (0.0, 0.5, 1.0, or 2.0 nightlights) on a particular night ($n = 12$) and control birds exposed to one nightlight on the same night ($n = 12$). One asterisk indicates a significant difference at $P < 0.04$ and two asterisks indicate a significant difference at $P < 0.02$ by a repeated measures MANOVA.

in both migratory stages (autumnal: illumination at source and an interaction of illumination at source by group, all $F_{3,20} \geq 3.5$, all $P < 0.04$; vernal: illumination at source and an interaction of both variables, all $F_{3,20} \geq 4.5$, all $P < 0.02$; Fig. 2).

TABLE 1. Measures (mean $\pm$ SE) of morphology and food intake of captive White-crowned Sparrows during the vernal and autumnal migratory stages. An asterisk denotes a significant difference from the vernal stage at $P < 0.02$.

Migratory stage (n)	Mass (g)	Fat score	Food intake (g day^{-1})	Rate of intake (g hr^{-1} daylight)
Autumnal (7)	29.9 $\pm$ 1.3	3 $\pm$ 0*	8.7 $\pm$ 0.5	1.1 $\pm$ 0.1*
Vernal (7)	32.1 $\pm$ 1.3	4 $\pm$ 0	7.9 $\pm$ 0.4	0.4 $\pm$ 0.0

TABLE 2. Measures (mean $\pm$ SE) of body mass, fat score, and daily food intake of captive White-crowned Sparrows over three days during the autumnal migratory stage, with food restriction occurring on Day 2. One asterisk denotes a significant difference from controls at $P < 0.02$, two asterisks denote a significant difference from controls at $P < 0.004$, and three asterisks denote a significant difference from controls at $P < 0.001$.

Measure Group (n)	Day 1	Day 2	Day 3
Body mass (g)			
Control (6)	29.9 $\pm$ 1.7	29.5 $\pm$ 1.5	29.4 $\pm$ 1.6
Experimental (6)	26.9 $\pm$ 0.1	23.8 $\pm$ 1.1***	25.3 $\pm$ 0.9
Fat score			
Control (6)	3 $\pm$ 0	3 $\pm$ 0	3 $\pm$ 0
Experimental (6)	3 $\pm$ 0	2 $\pm$ 0**	2 $\pm$ 0*
Food intake (g day ⁻¹)			
Control (6)	7.8 $\pm$ 0.6	7.5 $\pm$ 0.5	7.3 $\pm$ 0.6
Experimental (6)	6.8 $\pm$ 0.6	0.0 $\pm$ 0.0	6.0 $\pm$ 0.6

FOOD RESTRICTION

Autumn: morphology and locomotor activity. Food restriction resulted in a decrease in body mass and fat scores of experimental group birds relative to fed controls (effect of day and interaction of day by group, all $F_{2,9} \geq 47.2$, all $P < 0.001$; fat score day 2 and interaction, all $F_{2,9} = 13.8$, all $P < 0.004$; fat score day 3 all $F_{2,9} \geq 6.3$, all $P < 0.02$; Table 2). Daily food intake of controls did not vary over the three days ($F_{2,4} = 3.1$, $P = 0.16$). Comparing consumption between control and food-restricted birds on days 1 and 3 showed no significant differences of day or interaction of variables (all $F_{1,10} \leq 2.7$, all $P \geq 0.13$), as food-restricted birds ate quantities comparable to controls upon refeeding. Food restriction resulted in increased locomotor activity in afternoon and morning periods when tested over the three days (afternoon: the effect of day and interaction of both variables, all $F_{2,9} \geq 6.0$, all $P \leq 0.03$; morning: all $F_{2,6} \geq 5.2$, all $P < 0.04$; Table 3). No significant locomotory changes occurred during the night (all $F_{2,9} \leq 2.9$, all $P \geq 0.11$).

Autumn: behavior and location. As there were no group distinctions in the rest parameter during each session on the day of food restriction (all $t_8 \leq 1.8$, all $P \geq 0.12$), values were combined for both groups (Fig. 3). Comparisons across the four sessions revealed that birds spent proportionally more time at rest during the early night (Session 2; $\chi^2_3 = 12.0$, $P = 0.007$), identified as the quiescent phase, than during either day session (S 1, S 4: all $z = 2.2$, all $P < 0.03$). Beak-up flight was observed in both groups only during the late night (Session 3; $\chi^2_3 = 12.0$, $P < 0.008$) and without distinction between groups ($z = -0.9$, $P = 0.35$). However, beak-up was greater in the food-restricted birds than controls in both the late night and early morning sessions ($t_7 = -3.7$, $P < 0.01$ and $z = -2.3$, $P = 0.03$, respectively). During the daylight hours (Sessions 1, 4),

TABLE 3. Locomotor activity (average movement across an electronic beam min⁻¹ 30 min⁻¹ interval $\pm$ SE) of captive White-crowned Sparrows by daily period over three days during the autumnal migratory stage, with food restriction occurring on Day 2. One asterisk indicates a significant difference from controls at $P < 0.04$ and two asterisks indicate a significant difference from controls at $P < 0.03$.

Period Group (n)	Day 1	Day 2	Day 3
Afternoon			
Control (6)	56.5 $\pm$ 189.0	39.8 $\pm$ 19.6	32.8 $\pm$ 10.2
Experimental (6)	47.0 $\pm$ 13.9	297.3 $\pm$ 67.3**	64.4 $\pm$ 6.9
Night			
Control (6)	321.2 $\pm$ 110.1	316.5 $\pm$ 120.7	162.9 $\pm$ 38.5
Experimental (6)	375.8 $\pm$ 128.4	818.1 $\pm$ 226.7	248.9 $\pm$ 146.9
Morning			
Control (6)	15.7 $\pm$ 6.6	21.8 $\pm$ 9.3	14.3 $\pm$ 6.1
Experimental (6)	39.9 $\pm$ 13.0	99.5 $\pm$ 20.2*	27.0 $\pm$ 4.7

controls fed while experimental birds could not (all $t_6 \leq 3.2$, all $P < 0.03$). At these times, food-restricted birds were actively flying more than controls in the morning session ($t_7 = -13.0$, $P < 0.01$). With escalated activity, food-restricted birds were observed more frequently in the upper reaches of the cage (above perch) in the late afternoon (Session 1; $z = -2.4$, $P < 0.02$; Fig. 4). During both night sessions, all birds remained on their perches, which they used for resting, beak-up, or beak-up flight ($\chi^2_3 = 13.8$, $P < 0.002$). The following morning, controls were predominantly found feeding below the perch at the food dishes or on the floor ($\chi^2_3 = 8.6$, $P < 0.04$), while food-restricted birds moved continually between food dishes and the upper reaches of the cage.

Vernal: morphology and locomotor activity. Withdrawal of food resulted in decreased body mass and fat scores of experimental birds compared to those of controls (effect of day and interaction of day by group, all $F_{2,9} \geq 52.7$, all $P < 0.001$; fat score, all $F_{2,9} \geq 5.1$, all $P < 0.04$; Table 4). Food consumption of controls varied daily ($F_{2,4} = 18.5$, $P < 0.01$; day 1 vs. day 3, $t_5 = 6.8$, $P < 0.01$). Comparisons on days 1 and 3 of control and food-restricted birds indicated only a change over time ($F_{1,10} = 18.1$, $P < 0.002$). Food restriction increased locomotor activity in the afternoon and morning periods when tested over the three days of the experiment (afternoon: the effect of day, $F_{2,9} = 7.8$, $P < 0.02$, without an interaction of day by group, $F_{2,9} = 2.7$, $P = 0.12$; morning: effect of day and interaction of both variables, all $F_{2,9} \geq 6.5$, all $P < 0.02$; Table 5). No differences were detected during the night (effect of day and interaction of both variables, all $F_{2,9} \leq 2.7$, all $P \geq 0.12$).

Vernal: behavior and location. The quiescent phase was observed in all birds in the late afternoon (Session 1), as birds rested over 90% of the time (Fig. 5). Both groups maintained elevated levels of rest throughout the night sessions (S 2, S 3),

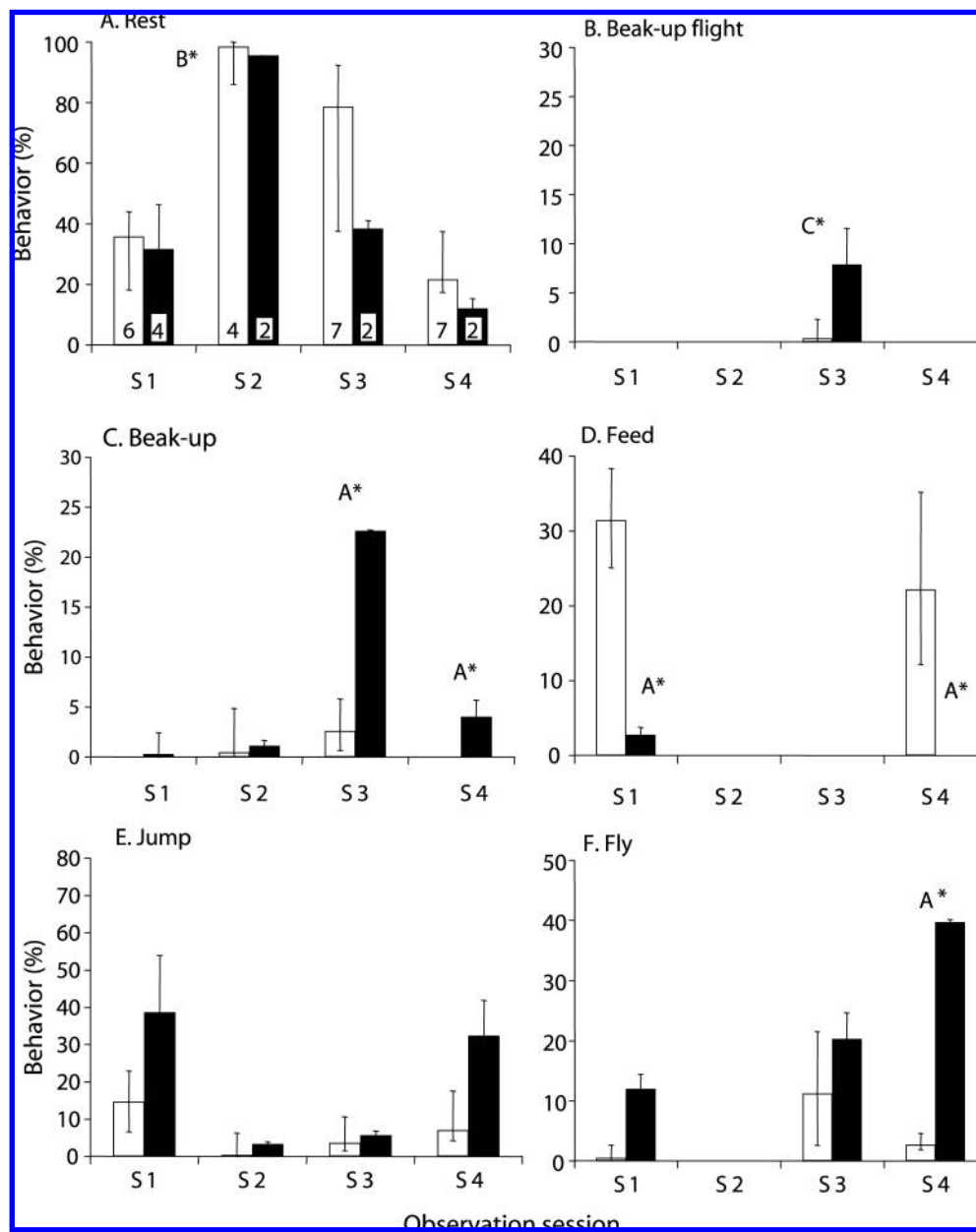


FIGURE 3. Observed behaviors of: (A) rest, (B) beak-up flight, (C) beak-up, (D) feed, (E) jump, and (F) fly in captive White-crowned Sparrows during the autumnal migratory stage during the four daily observation sessions on the day experimental birds (filled bars) were food-restricted and control birds (unfilled bars) were fed normally. Each frame (A–F) represents the percentage of the specified behavior over the other five behaviors observed within a behavioral observation session. Divisions of the 2 hr observation sessions include: S 1 = late afternoon, S 2 = early night, S 3 = late night, and S 4 = morning. Sample sizes are indicated in frame A. Note that the scales of the y axes vary across frames. The letter A indicates a statistical difference with the control group in a session according to the Wilcoxon test; the letter B indicates a significant difference of both control and experimental groups within the daily sessions (S 1, S 4); and the letter C denotes a significant difference in both groups within all other sessions by Friedman's test. An asterisk denotes a significant difference at $P < 0.03$.

but rest declined in the morning hours (S 4), with controls resting more than food-restricted birds ($t_{12} = 2.2$, $P < 0.05$). This discrepancy was explained by greater activity exhibited by food-restricted birds, who jumped and flew more than

controls (jump: $t_{12} = -2.2$, $P < 0.05$; fly: $t_{12} = -2.2$, $P < 0.05$). Only controls were able to feed, and fed significantly more during the morning (S 4) than the late afternoon session (S 1; $z = -2.4$, $P < 0.03$). All birds displayed beak-up flight and

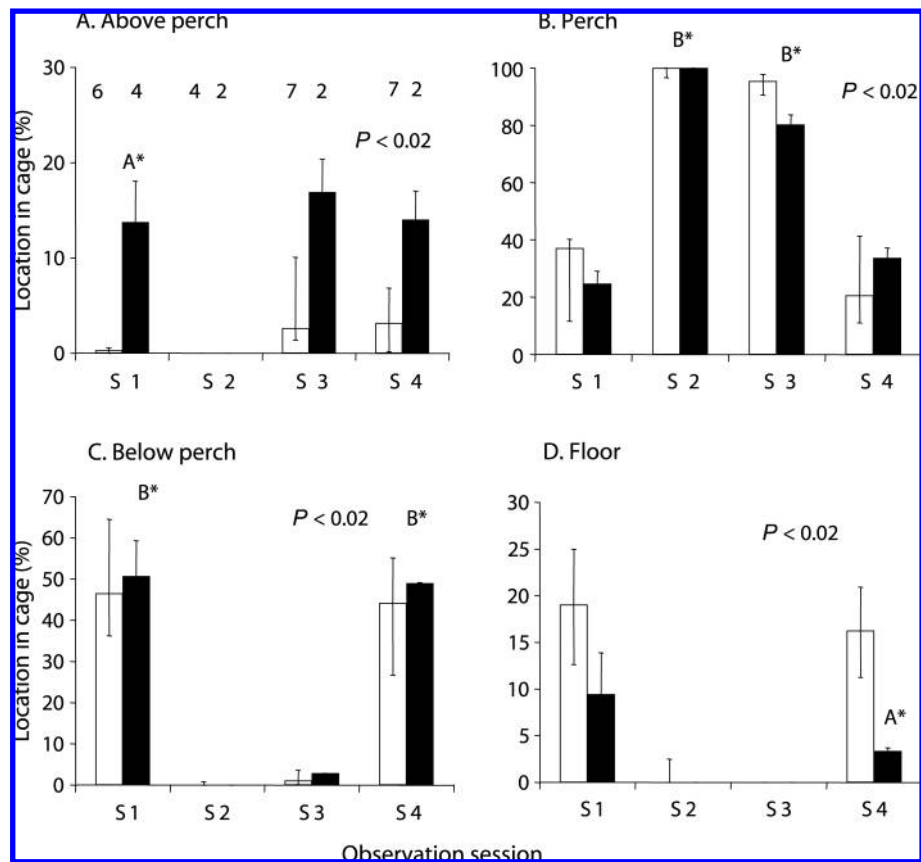


FIGURE 4. Throughout the four daily sessions (S 1–S 4; see Figure 3 for explanations), captive White-crowned Sparrows during the autumnal migratory stage were observed in specific locations within the cage, namely: (A) moving above the perch, (B) located on the perch, (C) below the perch at the food and water dishes, and (D) positioned on the floor. Each frame (A–D) represents the percentage of the specified location over the other three locations in the cage within each behavioral observation session on the day the experimental birds (filled bars) were food-restricted while the controls (unfilled bars) were fed normally. Sample sizes are indicated in Frame A. Note that the scales of the y axes vary across frames. The letter A indicates a statistical difference with the control group in a session by the Wilcoxon test. The letter B indicates a significant difference of both control and experimental groups with the other two sessions (Friedman's test), and an asterisk indicates significance at the level given in each frame.

beak-up during the night (S 2, S 3: $\chi^2_3 = 27.6$, $P < 0.001$, $\chi^2_3 = 31.7$, $P < 0.001$, respectively) without distinctions between the two groups (beak-up flight: all $z \leq 0.3$, all $P \geq 0.6$; beak-up: all $z \leq -0.5$, all $P \geq 0.3$). Spatially, the perch served as a site for rest and a platform for beak-up and beak-up flight until the morning session (S 4; $\chi^2_3 = 29.0$, $P < 0.001$), when levels of activity changed (Fig. 6). Food-restricted birds were observed more frequently above the perch in the morning than in the other sessions ($z = -2.5$, $P < 0.03$). Both groups were located primarily below the perch or on the floor ($\chi^2_3 = 30.4$, $P < 0.001$ and $\chi^2_3 = 25.6$, $P < 0.006$, respectively). The major distinction between groups was that controls either rested or fed while food-restricted birds moved continuously throughout the cage (Fig. 6). Exemplars of behavior may be viewed at <http://faculty.washington.edu/mramenof/movies/FoodRestriction.html>.

DISCUSSION

NOCTURNAL ILLUMINATION

Previous studies have suggested that atmospheric and climatic conditions influence migratory activity (Moore 1986, 1987, Gauthreaux 1991, Bowlin et al. 2005). In the absence of any nocturnal light (0 lux), locomotor activity in captive White-crowned Sparrows was suppressed and birds exhibited very limited movement. In both migratory stages, increasing the intensity of the illumination source resulted in greater frequencies of nocturnal locomotor activity. Such changes were attributable to subtle variations of <1 lux at the cages. Sensitivity to low levels of illumination has been shown in Black-capped (*Sylvia atricapilla*) and Garden Warblers (*S. borin*), which responded with increased migratory restlessness to light levels as low as 0.005 lux (Czeschlik

TABLE 4. Measures (mean $\pm$ SE) of body mass, fat score, and daily food intake of captive White-crowned Sparrows over three days during the vernal migratory stage, with food restriction occurring on Day 2. One asterisk indicates a significant difference from controls at $P < 0.04$, two asterisks indicate a significant difference from controls at $P < 0.001$, and three asterisks indicate a significant difference from Day 3 at $P < 0.002$.

Measure Group (n)	Day 1	Day 2	Day 3
Body mass (g)			
Control (6)	30.7 $\pm$ 0.9	30.2 $\pm$ 0.8	29.9 $\pm$ 0.8
Experimental (6)	30.9 $\pm$ 1.5	26.7 $\pm$ 1.5**	28.1 $\pm$ 1.4
Fat score			
Control (6)	3 $\pm$ 0	3 $\pm$ 0	3 $\pm$ 0
Experimental (6)	3 $\pm$ 0	2 $\pm$ 0*	3 $\pm$ 0
Food intake (g day ⁻¹)			
Control (6)	6.6 $\pm$ 0.3***	7.0 $\pm$ 0.4	7.4 $\pm$ 0.3
Experimental (6)	6.2 $\pm$ 0.2***	0.0 $\pm$ 0.0	7.6 $\pm$ 0.7

1977). Taken together, these results imply that nocturnal migrants respond behaviorally to small alterations in low levels of nocturnal illumination, offering support for the premise that the amount of moon- and starlight could affect migratory activity.

Under natural conditions complete darkness is an uncommon occurrence, as there is always some form of light, including the moon, stars, and reflection off clouds, bodies of water, or other topographical features, natural or otherwise. Even nocturnal species such as Tawny (*Strix aluco*) and Barn Owls (*Tyto alba*) rarely move in darkness unless they are familiar with their surroundings (Martin 1990a; T. Goldsmith, Yale University, pers. comm.). The range of nocturnal illumination varies extensively (up to 12 000-fold) owing to season, phase of the moon, starlight, topography of the landscape, climatic conditions, and altitude (Martin 1990a, 1990b). As captive White-crowned Sparrows appear to respond behaviorally to slight changes in nocturnal illumination, we suggest that this variation may provide critical information about current conditions, such as cloud cover and storm activity, that could influence a migrant's decision to depart or land.

Although the sensitivity of the visual system of birds is reported to be no better than that of humans (Martin 1990a), it is possible that seasonal changes in the visual system of nocturnal migrants may contribute to better acuity during the migratory stages. White-crowned Sparrows utilize celestial cues as well as the earth's magnetic field for orientation and navigation (Mewaldt 1964, Åkesson et al. 2001). These cues may be used independently or in concert with light-sensitive cryptochromes identified in the retinal ganglia of Garden Warblers (Mouritsen et al. 2004). Magnetic compass orientation is known to be a low-level light-dependent process that includes a radical-pair mechanism in Garden Warblers as well

TABLE 5. Measures of locomotor activity (average movement across an electronic beam min⁻¹ 30 min⁻¹ interval $\pm$ SE) of captive White-crowned Sparrows by daily period over three days during the vernal migratory stage, with food restriction occurring on Day 2. One asterisk indicates a significant difference over time at $P < 0.02$ and two asterisks indicate a significant difference from controls at $P < 0.02$.

Period Group (n)	Day 1	Day 2	Day 3
Afternoon			
Control (6)	50.0 $\pm$ 8.8	73.3 $\pm$ 10.4	44.8 $\pm$ 9.0
Experimental (6)	105.4 $\pm$ 24.2	188.0 $\pm$ 38.5*	80.4 $\pm$ 18.6
Night			
Control (6)	389.4 $\pm$ 94.4	398.2 $\pm$ 86.5	378.5 $\pm$ 87.8
Experimental (6)	367.5 $\pm$ 86.0	364.2 $\pm$ 93.9	262.7 $\pm$ 60.4
Morning			
Control (6)	289.5 $\pm$ 94.2	387.5 $\pm$ 95.0	280.7 $\pm$ 70.4
Experimental (6)	358.6 $\pm$ 71.6	692.3 $\pm$ 121.4**	205.5 $\pm$ 48.7

as an iron-containing receptor in the upper beak of European Robins (*Erithacus rubecula*; Ritz et al. 2004, Wiltschko and Wiltschko 2007, Stapput et al. 2008). Thus, the lack of movement of White-crowned Sparrows held in complete darkness may have been because neither the visual nor magnetic system was functional.

FOOD RESTRICTION

The impact of food restriction on migratory behavior has been studied in a number of long-distance migrants that cross such ecological barriers as the Saharan Desert in extended flights, including Spotted Flycatchers (*Muscicapa striata*) and Garden Warblers (Biebach 1985, Biebach et al. 1986, Gwinner et al. 1988). Restricting the food of birds in captivity until low body mass is reached results in increased nocturnal locomotor activity of autumn migrants, but once food is replenished, levels of nocturnal activity decline (Fusani and Gwinner 2004). Such responses allow birds to escape locations devoid of food but to cease nocturnal activity when it is available. Thus, we predicted that White-crowned Sparrows, a short-bout migrant, might react similarly to food restriction. However, withdrawal of food for 24 hr, which resulted in decreased body mass and fat stores, had no effect on either nocturnal locomotor activity or beak-up flight behavior. Yet, beak-up behavior increased during the later portions of the night and the following morning during the autumnal stage, which suggests that this behavior may be related to escape rather than migratory behavior per se, as food-restricted birds flew about the cage while controls fed. Our data offer support for the "emergency life history stage model," which states that organisms respond to unpredictable perturbations, such as depression of available food, by moving away from the immediate area to sites of abundance (Wingfield et al. 1998). Furthermore, the behavior of spring

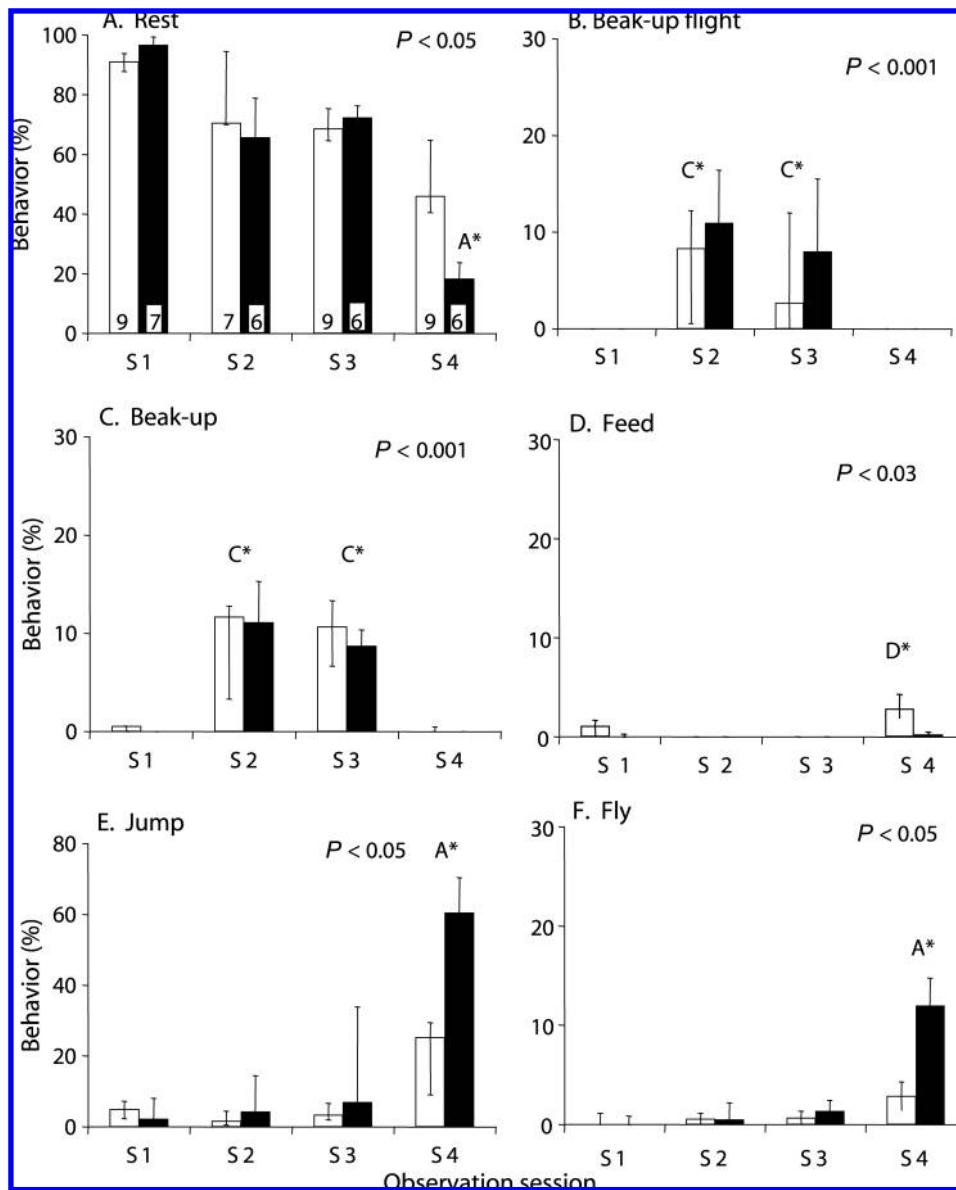


FIGURE 5. Observed behaviors of: (A) rest, (B) beak-up flight, (C) beak-up, (D) feed, (E) jump, and (F) fly in captive White-crowned Sparrows during the vernal migratory stage during the four daily observation sessions on the day experimental birds (filled bars) were food-restricted and control birds (unfilled bars) were fed normally. Each frame (A–F) represents the percentage of the specified behavior over the other five behaviors observed within the 2 hr behavioral observation session. Sample sizes are indicated in Frame A. Note that the scales of the y axes vary across frames. Sessions (S) are explained in Figure 3. The letter A indicates a statistical difference with the control group in a session (Wilcoxon test). The letter C denotes a significant difference of both groups with all other sessions (Friedman's test), and the letter D indicates a significant difference with S 1 among the control birds (Wilcoxon sign rank test). An asterisk denotes significance at the level given in each frame.

migrants that have just completed a flight across the Gulf of Mexico and landed along the coast of Louisiana, USA, offers additional evidence. Upon landfall, Red-eyed Vireos (*Vireo olivaceus*) forage widely throughout the vegetation (Loria and Moore 1990). Length of stay at this stopover site is related to body condition; lean birds remain longer than fatter ones. Also, captive studies of various North American

migrants indicate that lean arrivals to the Gulf Coast in spring show more locomotor activity during the day than at night in comparison with fatter birds (Yong and Moore 1993). Our results describe in detail both the timing and specific behaviors associated with increased locomotor activity of lean migrants. Thus, we suggest that both ecological conditions and fuel stores may influence whether a migrant will remain in an

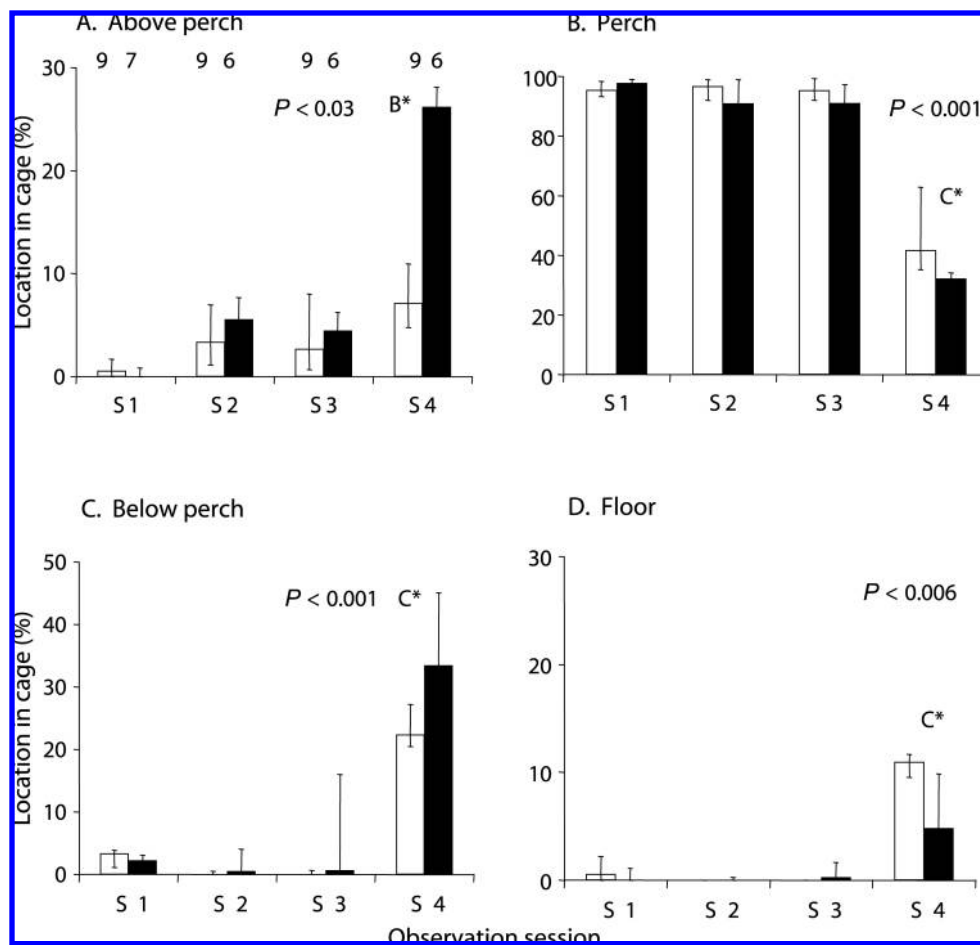


FIGURE 6. Throughout the four daily sessions (S 1–S 4, explained in Figure 3), captive White-crowned Sparrows during the vernal migratory stage were observed in specific locations within the cage, namely: (A) moving above the perch, (B) located on the perch, (C) below the perch at the food and water dishes, and (D) positioned on the floor. Each frame (A–D) represents the percentage of the specified location over the other three locations in the cage in each behavioral observation session on the day the experimental birds (filled bars) were food-restricted while the controls (unfilled bars) were fed normally. Sample sizes are indicated in Frame A; note that the scales of the y axes vary across frames. The letter B denotes a significant difference with the other three sessions among the restricted birds (Friedman's test). The letter C denotes a significant difference in both groups in comparison with the other three sessions (Friedman's test), and an asterisk denotes significance at the level given in each frame.

area to forage or continue migratory flight. For the short-bout migrant that does not cross ecological barriers, a 24 hr food restriction may be insufficient to inhibit migratory restlessness, given the prospect of feeding at daylight. These results offer a distinction in how short- and long-bout migrants respond to environmental conditions during migration.

Other studies investigating the behavioral and endocrine responses to food restriction also have shown that White-crowned Sparrows respond with increased locomotor activity (Merkel 1966, Astheimer et al. 1992, Lynn et al. 2003). Birds that had been forced to fast showed an increase in daytime locomotor activity compared to controls immediately following food removal at dawn (Lynn et al. 2003). This behavioral effect was diminished late in the day during the quiescent phase and throughout the night, but resumed at daylight. Plasma

levels of total corticosterone (steroid bound to and free of corticosterone binding protein) peaked the following morning after 22 hr of fasting (Lynn et al. 2003). Catabolic degradation of corticosterone binding protein resulted in elevated levels of free corticosterone. Free steroid is proposed to have a greater effect on cellular function than that bound to corticosterone binding protein (Breuner and Orchinik 2001). Although our experimental design varied from that of Lynn et al. (2003), taken together these results suggest that elevated free corticosterone may influence escape behavior, which includes beak-up and flights about the cage. The beak-up position may provide views of the immediate surroundings to avoid collisions with vegetation or show other topographic and celestial features to expedite escape. It is not clear why beak-up behavior was elevated only in autumn. Possibly lower fat stores played a role,

as it took longer for birds in the autumn study to replenish fat deposits after 24 hr of food restriction. Birds ingest food at a higher rate in autumn than in spring, suggesting an ability to adjust intake according to duration of available light, but there are limits. We surmise that birds may suffer from reduced feeding time when daylengths are short. Thus, autumn migrants may be more vulnerable to insufficiencies of food than spring migrants. A more complete analysis of this issue is warranted.

QUIESCENT PHASE

The state of motionless aphagia serves as a transition between daytime foraging and accumulation of nutrients and the onset of migratory flight when fuels are mobilized. Whereas locomotor and behavioral activities increased with food restriction, the quiescent phase in both the autumnal and vernal stages remained unaltered. Food-restricted birds in autumn fed continuously until lights were extinguished but then became quiet before initiating migratory restlessness around 21:00. Food-restricted birds in the vernal study ceased activity during the final 1.5 hr of daylight. Furthermore, Morton (1967) found that birds retained the spring quiescence up to a limit of 9 hr of food restriction. In spring, migrating *Catharus* thrushes sit quietly in woodlots in the midwestern U.S. late in the afternoon and in the early evening prior to departure after dark (Cochran et al. 2004). During this time, it has been reported that migrants obtain orientation cues from the setting sun (solar compass or polarized light) at dusk (Krantz and Gauthreaux 1975, Moore 1987, Cochran et al. 2004). Such results highlight the importance of the quiescent periods and suggest that they may serve to allow for completion of anabolic functions and accumulation of environmental information relevant to orientation prior to departure. Additionally, these periods appear to be somewhat resistant to restricted feeding opportunities prior to departure.

In support of the general hypothesis that migrants in the mature capability phase rely on environmental cues to regulate daily behaviors, captive migratory White-crowned Sparrows responded to variations in nocturnal illumination and availability of food. Our results confirm that birds increase the frequency of locomotor activity with enhanced nocturnal illumination. Contrary to our second prediction that food restriction would increase migratory restlessness, White-crowned Sparrows did not alter nocturnal migratory restlessness with food restriction in either migratory stage, except for the beak-up behavior exhibited in autumn. This distinction suggests that this behavior may be more associated with attempts to gain environmental information and escape rather than migratory restlessness. Plasticity of behavior may allow migrants to finely tune their progressive movements with local conditions. If food is available, pursuing it during the day would be the best option for refueling. Such calibration can increase the likelihood of successful completion of the migratory trip, as long as the variation in conditions remains within

the capacities of the migrants to respond. These results suggest that as changes in climatic and ecological conditions become more apparent globally, nocturnal, short-bout migrants may possess the flexibility necessary to allow for continual adjustments to alterations in the environment.

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