

Migratory behaviour of captive white-crowned sparrows, *Zonotrichia leucophrys gambelii*, differs during autumn and spring migration

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Summary

Gambel's white-crown sparrow (*Zonotrichia leucophrys gambelii*) is a long-distance, over-land migrant. In captivity birds display many characteristics of the autumn and spring migratory life history stages that include hyperphagia, fattening and high intensity nocturnal activity termed migratory restlessness or *Zugunruhe*. We recorded the behaviour of captive birds while simultaneously collecting 24 h locomotor activity. These data were used to define the behaviour displayed by captive birds during autumn and spring in order to compare the two migratory stages and to draw inferences for free-living birds. The predominant behaviour during day and nighttime was rest. Feeding occurred only during daylight hours but at a greater frequency in autumn than spring. Birds generally used their feet as the primary source of locomotion during the day termed 'jump'. During the night, two distinct behaviours, 'beak-up flight' and 'beak-up' involving high intensity wing motions were observed and considered components of migratory restlessness. The frequency of the 'beak-up flight' was greatest during spring and associated with the enhanced tempo of vernal migration. In both stages, migratory restlessness was preceded by a quiescent phase, the occurrence of which differed and related to time available for foraging and length of the night. Given these findings, we hypothesize that diel behaviours displayed by autumn and spring migrants in captivity highlight distinctions between the two life history stages.

Keywords: beak-up flight, beak-up, migratory behaviour, migratory restlessness, quiescent phase, *Zonotrichia leucophrys gambelii*.

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Introduction

Migration is the annual travel to breeding sites in spring and nonbreeding or wintering areas in autumn. Many approaches have been employed to study bird migration and have contributed to the understanding of its evolution, physiology and orientation (Alerstam, 1990; Berthold, 1996). Until recent advances in biotelemetry (Cooke et al., 2004; Bowlin et al., 2005; Cochran & Wikelski, 2005), tracking small and mobile individuals during migration has been problematic. Much of what is known in specific areas as physiology, competition, vigilance and diet selection has been accomplished by focusing on captive subjects (Biebach, 1985; Moore & Simm, 1985; Gwinner, 1986; Schwabl & Farner, 1989; Savard et al., 1991; Ramenofsky et al., 1999; Wiltschko & Wiltschko, 2003). Yet, very little is known of the actual behaviours displayed by migrants. To help rectify this, we studied the behaviour of captive migrants.

Gambel's white-crown sparrows (*Zonotrichia leucophrys gambelii*) (GWCS) are long-distance, short-bout migrant that breed from the Canadian-US Border into the arctic tundra and taiga habitats of Alaska and Canada and over-winter from the continental US into northern Mexico (Blanchard & Erickson, 1949; Wingfield & Farner, 1980). Birds are classified as nocturnal migrants and are reported to feed by day (Morton, 1967). By combining 24 h locomotor records and behavioural observations of GWCS we have identified general patterns of activity for both autumn and spring migratory stages (Ramenofsky et al., 2003; Landys et al., 2004a, b). Common to both, is the elevated nocturnal activity described as migratory restlessness or *Zugunruhe*. Preceding each bout of migratory restlessness is a period of quiescence. Additional behaviours contribute to the 24 h activity budget and may reflect seasonal distinctions but have not been well studied. We suggest that many of the behavioural displays of migrants in captivity can elaborate activities of free-living birds that are obscured during this highly mobile stage. Thus, we hypothesize that diel behaviours displayed by autumn and spring migrants in captivity would highlight distinctions between the two life history stages. Many have suggested that these stages differ markedly as the ecological and selective pressures that migrants face en route vary between the seasons (King & Farner, 1963; Drent et al., 2003). In spring, long distance migrants are confronted with increasing photoperiod and unpredictable climatic conditions that can impinge upon availability of food at high latitude

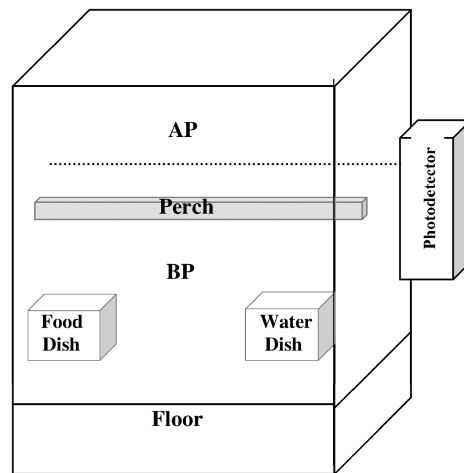


Figure 1. Diagram of cage equipped with photodetector and specific locations identified: Ap (above perch), Perch, Bp (area below perch with food and water hoppers), Floor of cage. Dotted line indicates infra-red beam emanating from and returning to photodetector.

and altitude. Furthermore, there are selective advantages, particularly for fit individuals, to arrive as early as possible – weather permitting – establish a territory, attract a mate, and produce an early clutch (Lack, 1968; Ketterson & Nolan, 1983; Wingfield, 1983; Drent et al., 2003). By contrast, in autumn daylength decreases and predictability of climatic conditions and food availability improve with distance from breeding areas. Therefore, we predict that the intensity of the migratory restlessness would be greatest during the spring stage in light of the strong selective pressures on birds at this time. Herein, we report results from behavioural studies on captive GWCS during the two life history stages of migration – autumn and spring.

Materials and methods

Capture and handling

GWCS were captured using mist nets during autumn migration at the Sunnyside Game Refuge in Central Washington State (46.1°N, 119.5°W) in September and October of 1999 and 2000. Following capture, birds were transported to the Department of Biology, at the University of Washington, Seattle, and held in outdoor aviaries exposed to natural conditions.

Conditions for captive studies

Selected at random, 20 birds of mixed ages and sex were banded and placed in individual cages (measuring $39 \times 34 \times 42$ cm) in one of two environmental chambers ($3.0 \times 1.8 \times 2.4$ m). Of the 10 birds in each chamber, six were held in registration cages equipped for recording 24 h locomotor activity (see below). Birds were held for 14 days to acclimate to the chamber conditions. The photoperiod used for the autumn studies was 8L:16D (Light:Dark, lights off 1700 h) that was conducted from September through November; locomotor activity of birds ($N = 6$) for autumn birds (see Figure 2A). By December, migratory behaviour subsided as birds no longer exhibited nocturnal activity (see Figure 2B) and had entered the winter life history stage. In March, spring studies were initiated when the same birds were exposed to a photoperiod of 18L:6D (lights off 1700 h). It is established that this manipulation induces development of the spring migratory life history stage (King & Farner, 1963; Wingfield & Farner, 1978; Landys et al., 2004a, b) (see Figure 2C). After approximately 60 days on this photoperiod, birds become photorefractory ceasing migratory restlessness and initiating prebasic moult (King et al., 1966; Wingfield & Farner, 1978) (see Figure 2D). Throughout the study, temperature in the environmental chambers ramped between 10° and 20°C daily with the minimum occurring at 0100 h and the maximum at 1300 h. Relative humidity was set at 50%. Each chamber was equipped with a Limelite Nightlight (Austin Innovations, Texas) placed above the cages mid-way in the chamber. While the intensity of light emitted at the source was 6.45 Lux recorded by a Weston Model 756 Illumination Meter (Newark, NJ), illumination recorded at cages positioned nearest to the Limelight was <1 Lux. This level of illumination was insufficient to photostimulate the birds after they had achieved photosensitivity in mid-December (Landys et al., 2004a, b). Throughout the experiment, birds were supplied water and *ad libitum* in food and water hoppers (Figure 1). Food was a mixture of Mazuri Chow (Nutrition International, Brentwood, Mo) and mixed seeds (University of Washington Custom Mix, Seed Factory NW, Inc., Kent, WA). Birds were given grit fortified with vitamins and minerals weekly (Bird Health Grit, Seed Factory, Ceres, CA). All conditions concerning bird capture, handling, and experimentation were performed according to the American Association of Accreditation of Laboratory Animal Care Guidelines and approved by the Institutional Animal Care and Use Committee at the University of Washington.

Locomotor activity recordings and analyses

Each of six registration cages in the two chambers was equipped with a photodetector (Radio Shack Alarm Entry, model #49-311) that emitted an infrared beam 34 cm above the bottom of the cage to a reflector (Figure 1). Movement in each cage was detected 0-10 cm above the central perch. As birds passed through the beam, an electric signal was transmitted to a Macintosh Computer. Analysis of locomotor activity was recorded by a Labview Computer Program (National Instruments Corporation, Austin, Texas) that was further refined by 'Perch Hopping Software' written by Dr. D. Baldwin, NMFS Seattle Washington. This program collects signals and computes an average movement per min over a 30 min interval referred to as locomotor activity.

For a more refined interpretation of the 24 h locomotor activity, we divided each record into three periods: Period I (P I) 1230 h to dark phase (Afternoon), Period II (P II) dark phase (Night), and Period III (P III) hours following night to 1100 h (Morning) (see Figures 2A, C). The mean of peak locomotor activity collated for each bird within each period was calculated. A one-way repeated measures ANOVA was used to compare locomotor activity across the three time periods. Sampling period was entered as a repeated factor. If significance was achieved, the multiple comparisons procedure, LSD test, was used to identify differences across the three periods. Where possible, the locomotor data were transformed using a \log_{10} calculation so that the data conformed to a normal distribution (Shapiro Wilke's W test with $p \geq 0.05$). If $p < 0.05$, then samples were analyzed using a Friedman's test to compare 3 related samples that were followed by Wilcoxon signed-rank test (WSR) using a Bonferonni correction for multiple comparisons where appropriate (Ramsey & Schafer, 2002).

The 24 h locomotor records were used for comparison of the two migratory stages. A phase of inactivity (quiescence) was identified preceding the elevated nocturnal levels of both the autumn and spring migratory life history stages (see Figures 2A, C). Quiescent was defined as a minimum of 2 consecutive intervals of 30 min duration with recorded activity of less than 1.8 average movements per minute or the limit of sensitivity of the photodetectors. For comparative purposes, intervals of quiescence were summed for each bird and an average duration (min) for all birds ($N = 12$) was calculated for both autumn and spring. Within individual comparisons across the autumn and spring were evaluated by Wilcoxon Sign Ranked test.

Table 1. Descriptions of behaviours and identified locations within the cage observed in captive Gamble's sparrows.

Behaviours	Descriptions
Rest (R)	Sitting in relaxed position, not moving within cage. May preen or move head without focusing in any direction
Jump	Locomotion, using feet for primary propulsion
Flight	Locomotion, using wings for primary propulsion
Beak-up Flight (BUF)	Bill pointing to near vertical with full wing beats (3-4 Hz) and may lift off perch
Beak-up (BU)	Bill pointing to near vertical without full wing beats and may move laterally along perch
Feed	Actively searching for food or water
Not Visible	Out of sight of observer
Other	Other behaviours not listed above
Locations	
Ab	Above perch, generally moving in the air or clinging to sides of cage
Perch	On perch
Bp	Area below perch, generally on food or water cups or in transition between these locations
Floor	On floor

The locomotor records identified relative changes in activity throughout three periods and helped to pinpoint times of interest that included the transitions between light and dark phases of the photocycle. To determine the specific behaviours displayed during these times, the 3 periods were divided further into four 2 h sessions (S): S I included the 2 h preceding lights out (1500-1700 h), S II the 2 h following lights out (1700 to 1900 h), S III the 2 h preceding lights on (0700-0900 h autumn; 2100-2300 h spring), S IV the 2 h following lights on (0900 to 1100 h autumn; 2300 to 0100 h spring) (Figures 2A, C). Two focal birds were filmed simultaneously during these sessions using a Sony Video HI 8 XR CCD-TRV87 Handycam with infra-red features.

Behavioural observations

Behavioural and location budgets (see Figures 4, 5) were developed from a preliminary study of the behaviour of captive birds (see Table 1). Rest was

classified as an inactive behaviour, while jump, flight, beak-up flight (BUF), beak-up (BU), feed, and other, were identified as active. Jump and flight involved movement from one location to another using feet or wings as primary mode of locomotion, respectively. Two distinct behaviours were beak-up flight and beak-up in which a bird would point its beak vertically either with or without full wing beats, respectively. To determine an association between behavioural displays and locations within the cage, bird's presence in specific areas within the cage were recorded as follows: Ab – positioned above perch, Perch – located on perch, Bp – positioned below perch, Floor – located on floor of cage (Figure 1).

Behavioural and location budgets were recorded for focal subjects using an instantaneous scan with 20 s intervals per 10 min session (Martin & Bateson, 1998). Each session occurred at intervals of 10, 30 and 50 min after each hour during the 4 h tapes. Behaviour and location data for each focal 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/h/period. The inter-observer reliability of behavioural recordings was tested by Pearson product moment correlation of observations made by two independent observers of two separate 10 minute video clips each with two focal birds ($r^2 = 0.889$, $df = 31$, $F = 113.2$, $p < 0.001$) (Martin and Bateson, 1998). All statistical analyses were carried out using SPSS 10.0 for Macintosh.

Results

Autumn

The locomotor activity recorded for 6 birds in the first week of October is presented in Figure 2A. The mean of peak activity during the night (26.21 ± 6.95 SE) exceeded both the preceding daylight hours (9.39 ± 2.96 SE) and following morning (11.15 ± 2.66) ($F_{2,6} = 10.65$, $p < 0.005$; WSR: $p < 0.05$). However, activity measured during the day did not progress directly into elevated levels at nightfall but ceased for approximately $120 \text{ min} \pm 11.31$ (Figure 3), a condition identified as the autumnal quiescent phase (Ramenofsky et al., 2003). After this interlude of quiescence, birds initiated nighttime activity that persisted until dawn at which time, activity decreased markedly.

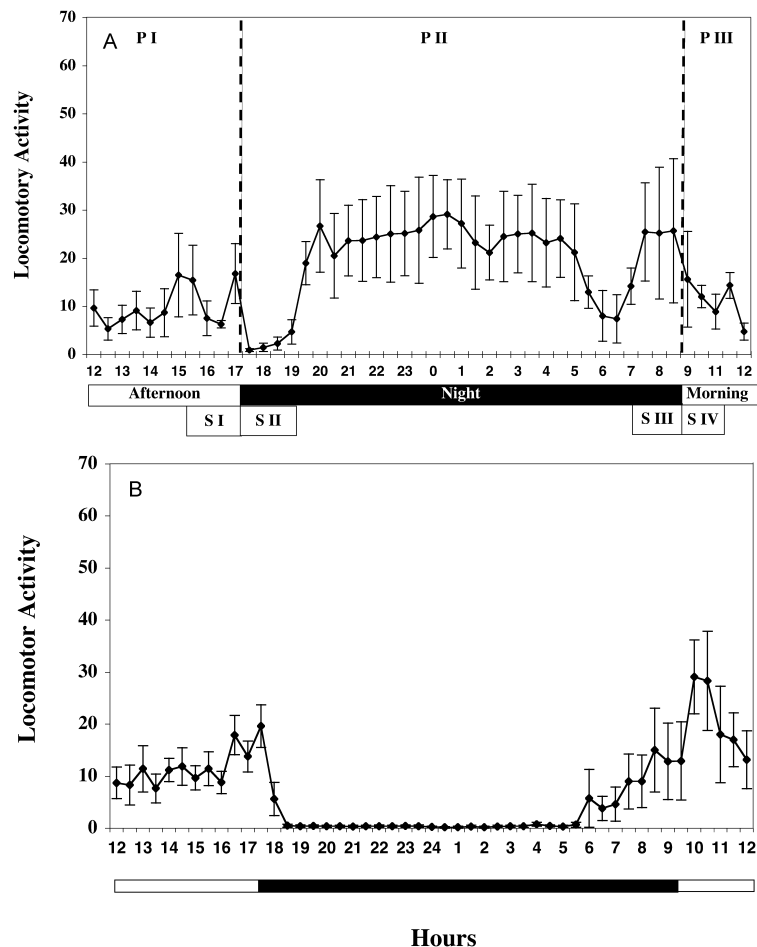


Figure 2. 24 h locomotor activity (average movement/min/30 min interval) recorded from birds in 4 life history stages, filled diamonds and error bars represent $X \pm SE$ for $N = 6$. Open bar below figure represents the light phase, filled bar is the dark phase. (2A) Locomotor activity during the autumn migration on a photoperiod of 8L:16D with lights out at 1700 h. Activity is divided into 3 periods: Period 1 (P I – afternoon hours from 12:30 to lights out, Period II (P II) night, Period III (P III) morning hours following night to 1100 h. S I through S IV indicate the 2 h sessions during which birds were videotaped during autumn stage: S I last 2 h light phase (1500–1700 h), S II first 2 h of dark (1700 to 1900 h), S III last 2 h of dark (0700 to 0900 h), S IV first 2 h of light (0900 to 1100 h). (2B) Illustrates birds measured during the winter life stage. (2C) Birds in the spring stage. Period I–III described in Fig. 2A. S I through S IV are 2 h videotaping sessions: S I last 2 h light phase (1500–1700 h), S II first 2 h of dark (1700 to 1900 h), S III last 2 h dark (2100 to 2300 h), S IV first 2 h of light (2300 to 0100 h). (2D) birds in pre-basic moult stage.

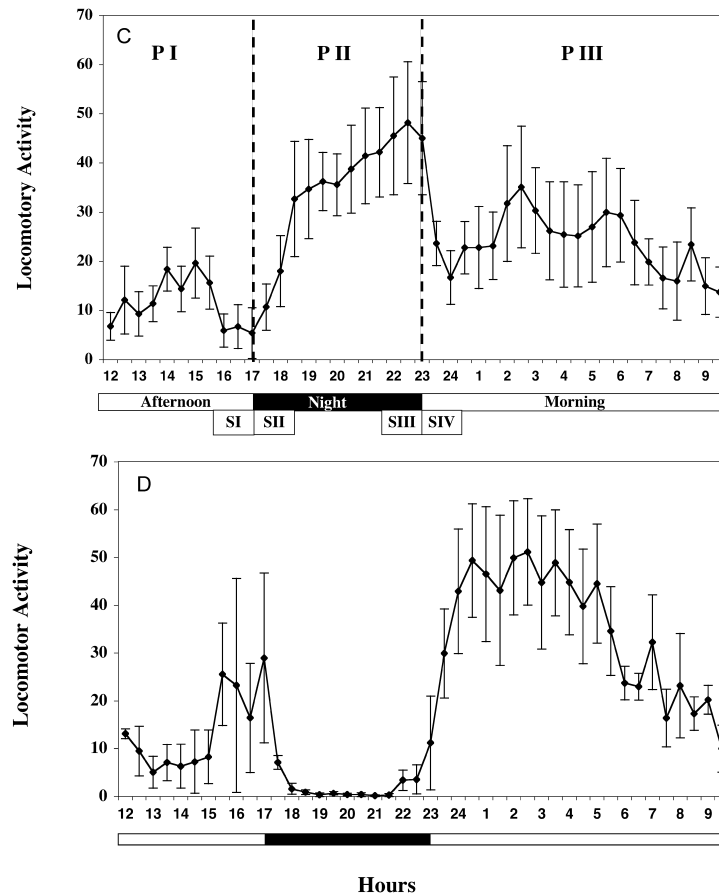


Figure 2. (Continued).

Behaviours displayed during the 4 observation sessions are presented in Table 1, Figure 4A and (<http://faculty.washington.edu/mramenof/movies/Daytimebehave.html>) and (<http://faculty.washington.edu/mramenof/movies/Nightbehave.html>). Rest, the inactive behaviour, was prevalent throughout all sessions, especially in S II & III. Feed, a prominent active behaviour, occurred only during the day (Sessions I & IV). The other major behaviours included jump and fly that were observed mainly in S I, III & IV. Two behaviours unique to the nighttime (S II & III) included beak-up flight (BUF) and beak-up (BU).

Data from the location budgets (Figure 5A) aligned SI & IV and were distinct from S II & III. During SI & IV, birds spend a smaller proportion of

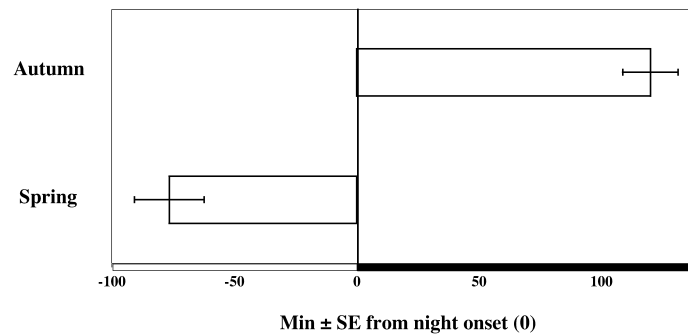


Figure 3. Comparison of the onset and duration of quiescent phase measured in all birds ($N = 12$) during autumn and spring migratory life-history stages. Horizontal columns and error bars represent the mean \pm SE of the duration (min) of the quiescent phase measured in relation to nightfall (0), Wilcoxon Signed Ranks test, $z_{12} = -3.94$, $p < 0.01$. Open bars represents light phase; filled bar dark phase of the 24 h cycle.

the time on the perch while either below perch or on floor, locations where birds feed and drink. During S II & III, the perch was the dominant location (>95% for both) upon which birds rested or negotiated beak-up flight and beak-up.

Winter

The 24 h locomotor records verified complete cessation of nocturnal activity at the conclusion of the autumn migratory stage (Figure 2B). This is the winter life history stage with birds held continuously on short day lengths of 8L:16D. Some activity is apparent in the early morning hours (from 0600 h on) but the frequency is far below nocturnal activity of the autumn migratory stage. Direct observations revealed that behaviours displayed are not migratory restlessness as neither beak-up flight nor beak-up were observed but consisted of jump and flight (M. Ramenofsky, pers. obs.). At dawn locomotor activity rises as birds commence to feed and move more generally about the cage. This pattern of activity persists until birds are exposed to long photoperiods (≥ 12 h of light/24 h).

Spring

After 15 days exposure to a photoperiod of 18L:6D, the locomotor activity of the spring stage emerged fully (Figure 2C). The mean of peak activity during the night (39.47 ± 6.89 SE) was significantly greater than that recorded

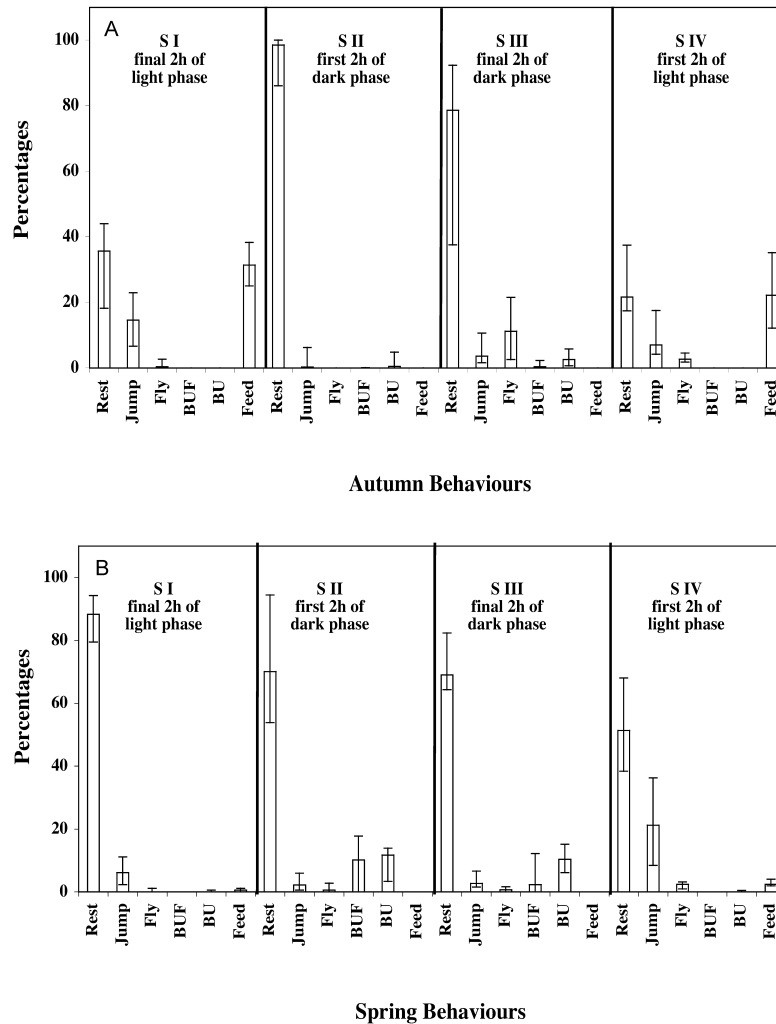


Figure 4. Percentages of total behaviours displayed by birds within the 4 observation sessions (I-IV) during autumn (4A) and spring stages (4B). Complete descriptions of sessions listed in Figures 2A, C. Columns represent median and ranges extending from the 25th to 75th quartiles for $N = 10$ in autumn and $N = 17$ in spring.

during the afternoon hours (11.43 ± 3.89) ($F_{2,6} = 6.21$, $p < 0.03$; WSR: $p < 0.01$) but not in comparison with that of the following morning (22.35 ± 6.98 ; WSR: $p > 0.05$). In late afternoon prior to lights off, the locomotor activity dropped significantly (Friedman's test: $\chi^2_{2,6} = 6.5$, $p = 0.039$) and

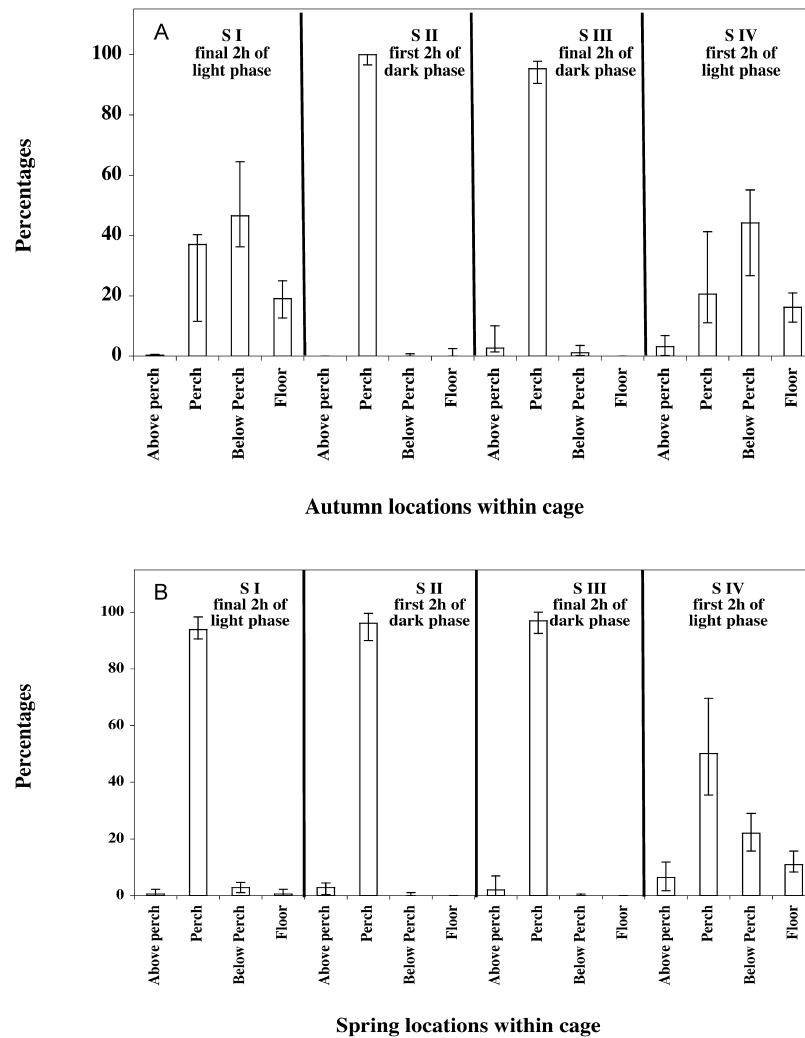


Figure 5. Percentages of total locations in which birds were observed within each of 4 observation sessions (I-IV) during autumn (5A) and spring (5B). Columns represent median and ranges extending from the 25th to 75th quartiles for $N = 10$ in autumn and $N = 17$ in spring.

remained low for approximately $76.5 \text{ min} \pm 14.18 \text{ SE}$ prior to lights out, a stage described as the springtime quiescence (Ramenofsky et al., 2003). At this time, birds ‘hunker down’ with bellies flush with the perch. Some birds sleep with the head tucked beneath the wing while others keep their head

upright and remain completely quiet. At lights out, birds commence intense nocturnal activity that persists throughout the night phase (S II & III).

Behaviours displayed during the 4 sessions are presented in Table 1 and Figure 4B. Rest was the predominant behaviour in all sessions, though it dropped in S IV. Feeding was observed only during the daylight hours (S I & IV). The other daytime behaviours including jump and fly were more prominent during Session IV. Again, the two active behaviours, beak-up flight and beak-up, were unique to the night, S II & III.

The perch appeared as the predominant location in all 4 sessions (Figure 5B). The S IV budget diverged from the others 3, with locations above and below perch and floor contributing to nearly 50% of the total budget.

Moult

After 60 days exposure to 18L:6D, birds become photorefractory and commence pre-basic moult (King et al., 1966; Wingfield & Farner, 1978; Ramenofsky & Wingfield, 2006). The 24 h locomotor record illustrates cessation of spring migratory stage with the disappearance of quiescent phase and migratory restlessness and elevated activity at dawn (Figure 2D).

Comparisons of autumn and spring migratory stages

Behaviour

Measurements of the onset and duration of the quiescent phases during the two migratory stages revealed differences (Figure 3). In autumn, the phase occurs in the early portion of the night while spring birds settle into quiescence at the end of the day prior to lights out. Seasonal comparisons of onset and duration of this phase were significantly different according to the Wilcoxon Signed Rank test, $z_{12} = -3.94$, $p < 0.01$. Nocturnal activity is present only during the migratory life history stages and behaviours contributing to it are primarily beak-up flight and beak-up (Figure 4A, B). Comparing frequencies of these behaviours displayed during the night phase (combining S II & III) indicated that beak-up flight (110.97 ± 16.88 , median \pm interquartile range, $N = 5$) was significantly greater in spring than autumn (0.00 ± 1.65 m, $N = 5$) according to the Wilcoxon signed-rank test ($z_{1,5} = -2.03$, $p < 0.05$). However, BU was comparable in both stages (Spring: 5.97 ± 8.00 , autumn: 1.85 ± 4.82) ($z_{1,5} = -1.48$, $p = 0.138$). In autumn, birds fed persistently until lights went out. But in spring, they

ceased feeding approximately 76.5 min prior to onset of darkness when they entered the quiescent phase. Autumn birds fed on average 25% of the time during Sessions I and IV; whereas, spring birds fed only 2% of the time during these sessions.

Locations

Observed locations within cage could be associated with birds' behaviour during both stages (Figures 5A, B). Birds residing above the perch were in motion, generally flying or jumping. When positioned on the perch, they rested but at night most used this location to initiate beak-up flight and beak-up. When located below perch, birds were either feeding or drinking. Activities on the floor involved either not visible, tearing paper or pecking at seeds. The location budgets provided additional support for the behavioural distinctions observed in autumn and spring during Session I. While spring birds were quiescent at this time, they were mainly located on the perch. Autumn birds however rested and fed during this session and were spread more generally throughout the cage from the floor, below or on perch. These distinctions may help elaborate the spatial and temporal variations of habitat use for free-living birds during both stages of migration.

Discussion

Integrating results from the 24 h locomotor records and behavioural observations of captive birds has revealed seasonal distinctions between autumn and spring migratory stages. Migratory restlessness displayed by birds in both migratory stages is comprised predominantly of beak-up flight and beak-up which are absent in other life history stages namely the winter and pre-basic moult. Prior to the onset of the migratory restlessness, birds settle into a period of quiescence in which the locomotor records are basal and birds reside at complete rest. Timing and duration of the quiescent phases are seasonally distinct. In autumn, birds remain active until lights are extinguished after which become quiescent for nearly 2 h when nocturnal activity begins. In spring, quiescence occurs before lights out and initiate nocturnal activity with onset of darkness.

Quiescent phase

Wagner (1930) and Palmgren (1949) initially identified a period rest or sleep of varying duration in a number of captive spring migrants that occurred prior to expression of migratory restlessness. Later, Morton (1967) reported that spring migrating GWCS ceased feeding late in the afternoon and roosted quietly in shrubbery prior to nocturnal departure. He suggested that suspension of activity allows for complete digestion of food reducing excess weight at take-off. Others have suggested that migrants obtain orientation cues from the setting sun (solar compass or polarized light) as they sit quietly at dusk (Krantz & Gauthreaux, 1975; Moore, 1987, Sandberg et al., 1991; Cochran et al., 2004). GWCS use solar and celestial cues for orientation during migration (Mewaldt, 1964; Åkesson et al., 1996, 2001, 2002). Taken together, the quiescent phase may serve as both a time to complete anabolic functions and accumulate environmental information relevant to orientation at time of departure.

Considering Palmgren's (1949) point that birds may sleep during the quiescent phase, our observations reveal that some birds tuck their heads beneath their wings suggesting sleep. Recently, Rattenborg et al. (2004) suggested that GWCS experience sleep deprivation during spring migration. Thus, quiescent phase may be a critical time for migrants to repay some of the mounting sleep debt accrued throughout migration but further investigations are needed.

Furthermore, quiescent phase may be considered a transitional state of metabolic and hormonal systems as birds progress from an anabolic state of feeding and digestion throughout the day to a catabolic condition of flight and fuel utilization at night (Morton, 1967; Ramenofsky et al., 2003; Landys et al., 2004a). Increased activation of lipid metabolic enzymes are associated with the switch from daytime feeding to nighttime flight in a closely related migrant, the dark-eyed junco (*Junco hyemalis*) (Ramenofsky, 1990; Savard et al., 1991; Ramenofsky et al., 1999). In terms of the endocrine system, baseline corticosterone, the prominent glucocorticoid in birds, rises from mid-day samples through the quiescent period and reaches a peak early in the night (dark phase) when birds display migratory restlessness in spring captive GWCS (Landys et al., 2004b). A similar pattern was found in captive dark-eyed juncos, sampled during the spring migratory stage (Ramenofsky et al., 1999). Additionally, baseline corticosterone rises sharply just prior

to departure from a month long stop-over in the Wadden Sea, Netherlands, in the bar tailed godwit, *Limosa lapponica* (Landys-Ciannelli et al., 2002). This increase in baseline corticosterone is associated with completion of the feeding phase of stopover and reabsorption of digestive organs, a weight reducing mechanism, immediately prior to departure for breeding grounds in Siberia 4000 km away (Landys-Ciannelli et al., 2002, 2003). Taken together we suggest that the quiescent phase is common to long distance migrants and may involve a concert of central and peripheral processes that affect smooth transitions from anabolism to preparation for catabolic activities of flight.

Timing of the quiescent phase differs in autumn and spring suggesting separate regulatory mechanisms. The fact that this phase precedes intense nocturnal activity in both stages implies that the components are linked. As GWCS are nocturnal migrants, length of the night may be the factor regulating timing the quiescent phase. Able (1993) suggested that free-living Savannah sparrows (*Passerculus sandwichensis*) fly for approximately 6-8 h per night during migration. This could represent a physiological limit of flight activity for overland migrants such as GWCS influencing the timing of the quiescent phase and subsequent take-off. Also, this may indicate reliance upon celestial cues apparent only during the dark phase of night since onset of migratory restlessness has been associated with decreased illumination (Wagner, 1937; Gwinner, 1967).

Migratory restlessness

The distinguishing feature of the migratory life history stages is intense nocturnal behaviour or migratory restlessness. Historically, this activity was monitored in registration cages (Wagner, 1930; Farner & Mewaldt, 1953; Eyster, 1954; Palmgren, 1949). These studies identified the timing of migration by recording duration and intensity of activity. Helpful as these studies have been, they lacked definition of actual nocturnal behaviours displayed by captive birds until the work of Berthold & Querner (1988) and Berthold et al. (2000) on garden and blackcap warblers (*Sylvia borin* and *atricapilla*). In these studies, birds were moving about the cage by hopping, climbing, fluttering, and flying, as well as beating their wings rapidly but not leaving the perch. The authors described this behaviour as 'flying with the brakes on' and attributed it to migratory restlessness or *Zugunruhe*.

In captive GWCS, the beak-up flight and beak-up were two prominent behaviours observed during nocturnal migratory restlessness. While birds

showed other active behaviours during the night, specifically flight and jump, we considered beak-up flight and beak-up to be specifically associated with migratory restlessness because both were unique to the night and confined to the migratory life history stages of autumn and spring. Flight and jump observed at night did not differ qualitatively from those exhibited during the day and thus were not behaviours specific to migratory activity but may be associated with it.

Both beak-up flight and beak-up were initiated primarily from the perch. From these vantages, birds would have an unobstructed view through the top of the cage. We attribute the beak-up posture to the birds' searching the sky for celestial cues for orientation or to obtain directional information of the earth's magnetic field as Mouritsen et al. (2004) have observed in garden warblers with head scans. Field observations during autumn migration in Central Washington State offer further support. At this time GWCS seek refuge in large numbers in dense foliage in the late afternoon then move at nightfall to more exposed low-lying brush. Under clear atmospheric conditions, individuals take-off from shrubbery at steep angles (S. Meddle, M. Ramenofsky, J.C. Wingfield, pers. obs.). Similar observations in terms of timing and departure have been made for other migratory species (Hebrard, 1971; Bolshakov & Bulyuk, 1999; Bolshakov et al., 2000; Sandberg et al., 1991).

While migratory restlessness was observed in both seasons, focal observations revealed less frequent and consistent beak-up flight and beak-up in autumn compared to that of spring. In autumn, some birds actively displayed migratory restlessness while others rested for the majority of the night. In contrast, during spring both were the predominant active behaviours during the night (Figure 4b). Several studies on captive migrants have suggested that autumn migration in free-living birds is less synchronous and intense than spring migration (King & Farner, 1963; King et al., 1966; Gwinner, 1986). The selective pressure on individuals to arrive promptly on the breeding grounds to establish territory and reproduce in the spring is greater than movement southward toward the wintering grounds in autumn (King & Farner, 1963; Ramenofsky et al., 2003). These ideas support our observations of seasonal differences in the intensity of displayed migratory restlessness. An alternative explanation for these data is that birds captured during autumn migration in Central Washington herald from different breeding populations

of birds (Ramenofsky & Hobson, unpubl. results). Although some individuals will continue to migrate further south, others have arrived at the northern edge of their wintering range nearing the end of the autumn migratory life history stage (Ramenofsky et al., 2003). This variation could contribute to the decreased level of migratory restlessness observed. By contrast, all birds in the spring stage were artificially photostimulated. This experimental manipulation serves to synchronize migratory functions of all birds in captivity as it probably serves a similar function in free-living conditions (Ramenofsky & Wingfield, 2006). These results point out the need for a better understanding of preparations and execution of autumnal migration in free-living birds.

Feeding

In this study, birds fed only during daylight hours. However, the frequency of feeding differed between the seasons. In autumn, birds fed persistently until lights went out. But in spring, they ceased feeding during the quiescent phase. This difference may be due to the relative lengths of daylight hours. With longer nights, autumn birds may be food restricted by the limited hours of daylight. In contrast, spring birds could spend a smaller percentage of time feeding during the day and still have sufficient time to ensure fueling. Rates of food intake measured in GWCS (g ingested/h) in autumn exceed that of spring birds (Ramenofsky et al., in prep.). Daily feeding requirements in autumn may drive the quiescent phase into the early portion of the night prior to nocturnal departure. The lengthening daylengths of spring could dictate duration of migratory flight, at least, in the early stages of migration. Thus, birds have sufficient daylight to feed leaving time at day's end for the transitional phase of quiescence.

Rest

Birds in captivity rest a large percentage of the time. During the day, captives intersperse rest with feeding and locomotion. A similar pattern can be observed during migration in free-living GWCS that forage in loose bands, moving from site to site, and resting during the day (M. Ramenofsky, pers. obs.). Unlike birds in the field, captives have free access to food and water requiring less time and energy to obtain. At night, they rest on the perch but when active, will exhibit predominantly beak-up flight and beak-up. Both behaviours involve continuous preparation for and execution of take-off, which

are the most energetically taxing component of flight (Bonser & Rayner, 1996; Pennycuick, 2003). Thus, the high incidence of rest may be a consequence of fatigue resulting from repeated attempts to take-off. It is assumed that once free-living birds take-off for a migratory bout, flight is continuous until they alight at daybreak.

In light of our hypothesis, migratory behaviour of captive GWCS reveal distinctions between the autumn and spring migratory stages. Timing and duration of quiescence preceding onset of migratory restlessness varied with stage. Suggested reasons for this distinction may be related to the duration of daylight – time available for birds to refuel. Expression of migratory restlessness, beak-up flight and beak-up, are confined to the two migratory stages. In light our prediction, the most active behavioural component of migratory restlessness, beak-up flight, occurred at a greater frequency during spring than autumn offering support for the suggestion that this stage is more intense and synchronized than autumn. Armed with seasonal distinctions, we now proceed to test the influence of specific environmental factors on migratory behaviour that will allow us to draw inferences about free-living birds during autumn and spring migration.

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