Contextual generality of roosttime restlessness in captive American robins (*Turdus migratorius*)

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A series of experiments with captive American robins examined factors affecting roosttime restlessness, that is, the burst of locomotor activity that appears at dusk and is thought to be a correlate of the communal roosting habit of this species. First, the restlessness occurred earlier on cloudy days than on sunny ones, suggesting the importance of illumination level in initiating the activity burst. Second, in studies on social effects, the restlessness was greater when robins were totally isolated than when they had visual-auditory access to conspecifics; indeed, when a small flock of robins was housed together, restlessness at dusk was suppressed completely. Third, the birds were more restless when they could see a human observer than when they could not, implying an interaction of fearfulness with the roosting tendency. Finally, restlessness occurred in a large flight cage as well as in small cages, as long as the birds were not maintained in a flock. In sum, roosttime restlessness appears to be a robust phenomenon that occurs under a wide range of laboratory conditions, but which also can be substantially influenced by numerous environmental variables. Further experimental examination of these variables may advance present understanding of the survival value of communal roosting in this species.

The daily activity pattern of captive American robins (*Turdus migratorius*) under conditions of natural illumination typically consists of moderate-to-high activity in the early daylight hours, a gradual decline in activity as the day progresses, and finally a brief period of high activity at dusk just before the birds settle down for the night (Eiserer, 1979; Palmer, 1970). Several lines of evidence suggest that the high activity at dusk is a behavioral correlate of the robin's tendency to fly to a communal roost each evening and sleep there with conspecifics.

First, free-living robins show a characteristic restlessness around dusk preliminary to their flights to the roost (Brewster, 1890). A comparable display of restlessness by captive robins might be expected, much as many songbirds show "migratory restlessness" on a seasonal basis, whether free-living or in captivity (Eyster, 1954). Second, the high activity of captive robins at dusk is often accompanied by an increase in the occurrence of wing-flapping which may represent flight-intention movements or an "urge to fly" (Eiserer, 1979). Third, the activity peak at dusk appears every month of the year (Eiserer, 1979; 1980c), a finding that is in agreement with field reports that wild robins travel to a communal roost during all four seasons (Black, 1932; Brewster, 1890; Howell,

1940; Speirs, 1957). Fourth, the activity peak at dusk ("roosttime restlessness") emerges ontogenetically at approximately the age when young wild robins would be expected to make their maiden flights to the roost (Eiserer, 1980a). Fifth, roosttime restlessness is suppressed in captive female robins who display a high tendency to incubate. This is consistent with the natural situation in which breeding females must spend nights on the nest to keep eggs warm (Eiserer, 1980d).

Despite this evidence, the fact remains that most research with captive robins has been limited to a restricted set of circumstances: The birds have been maintained in small cages, they have had visual access to a human observer, they have been in visual, but not auditory, isolation from conspecifics, and the observations have been made on essentially cloudless days. Given that each of these factors might influence the daily activity patterns of captive avians, it is important to determine whether roosttime restlessness is a phenomenon that occurs regardless of the birds' immediate environment or is instead the peculiar result of specific observational contexts.

EXPERIMENT 1A

The present experiment investigated whether the previously described activity pattern (a decline in activity across the daylight hours, and then an activity burst at dusk) would occur on days that were completely overcast. Speirs (1957) and Torrey (1890) agree that robins fly to the roost site earlier on cloudy evenings than on clear ones, while Brewster (1890)

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indicated that the birds may leave the roost later on cloudy than on clear mornings. Similar effects occur with other communally roosting species (Counsilman, 1974; Meanley, 1965; Seibert, 1951).

Captive robins, then, might simply be expected to awaken later and to show roosttime restlessness and retire earlier on cloudy days than on sunny ones. A somewhat different finding could be predicted from the effects that cloud cover has on the singing behavior of wild robins. Although robins normally restrict their singing to the low-illumination periods of early morning and evening, heavy clouds can initiate an outburst of song at midday (Wing, 1956, p. 333). This implies that low light intensity constitutes an important stimulus for the birds' singing behavior. If dim light is also important for the restlessness that normally occurs at dusk, then the birds might be unusually restless throughout the day during overcast weather. Experiment 1A, which compared the robins' day-long activity pattern on sunny vs. cloudy days, permitted an assessment of these possibilities.

Method

Subjects. Eight 2.5-year-old American robins (*Turdus migratorius*) served as subjects. These birds had been removed from their nests in the Amherst, Massachusetts, area when they were approximately 10 days old. Throughout their first 2 years of captivity, the robins were maintained on a LD 12:12 cycle. The present study was conducted in Penn Yan, New York, several months after the robins had been switched to a natural day-night cycle. More specifically, the birds were housed in individual cages in a room illuminated only by the sunlight entering a single window (50 × 75 cm). The cages (35 × 50 × 38 cm) provided continuous access to water and commercially prepared mynah bird pellets, and were equipped with two parallel perches that lay some 20 cm apart. Since the cages were separated by cardboard dividers, the robins were visually isolated from one another; however, since all the cages were kept in a single room, the birds could hear each other.

Procedure. Observations were taken on two separate days: March 13, 1977, when the weather was completely overcast and, in fact, included heavy snowfall for several hours, and March 15, 1977, when the weather was clear and sunny. On each of these days, the robins were observed for 8 min every 20 min, from 5:20 a.m. to 7:00 p.m. During these 8-min periods, the behavior of each robin was monitored for 60 sec (i.e., Robin 1 was observed during the first minute, Robin 2 during the second minute, etc.). Throughout the observation periods, the investigator sat quietly in a chair about 2 m in front of the cages, in plain view of all of the birds.

The robins' activities were quantified under two, largely complementary categories: (1) *perch hops*, the number of times per minute that a given bird moved from one of its perches to the other; and (2) *inactivity*, the number of seconds per minute that a given bird spent sitting quietly on its perch, not hopping back and forth, vocalizing, feeding or drinking, or flicking its tail or wings.

Results

The robins showed the same general activity pattern on both the cloudy day and the sunny day (Figure 1). The birds were completely inactive from 6:00 to 6:20 a.m., the time that represented the end of their sleeping period (i.e., they had not yet stirred for the day; and in fact the room was still dark). The

Figure 1. Group mean seconds of inactivity per minute (top) and group mean number of perch hops per minute (bottom) during both sunny and cloudy weather, as a function of time of day.

birds became relatively active during the early morning hours, but progressively less active as they entered a "loafing" period of extreme inactivity in the late morning and early afternoon. The loafing period, during which the birds spent 50-55 sec/min simply sitting quietly on their perches, ended abruptly at dusk, when the robins suddenly became very active. This roosttime restlessness lasted a short while before the robins settled down for the night.

The functions in Figure 1 suggest that the robins became active in the morning a little later on the cloudy day than on the sunny day and that they entered roosttime restlessness a bit earlier in the afternoon. These differences were slight and the data from the 2 days are otherwise essentially replicative of each other.

Discussion

The daily activity pattern delineated in the present study replicates previous findings with this species (Eiserer, 1979; Palmer, 1970) in that the robins showed a peak of morning activity which waned as the day progressed and then entered another period of high activity at dusk. This pattern is not unusual for captive avians generally (Eyster, 1954; Palmgren, 1949; Smith, Brown, & Mewaldt, 1969).

That the robins were not unusually restless on the

cloudy day does not imply that light intensity is unimportant in initiating roosttime restlessness. The dimming effects of clouds during most of the day may simply be inadequate to achieve a critical threshold level. Alternatively, the effects of light intensity may depend in an interactive way upon the operation of some biological clock. Still another possibility is that the crucial variable is not light intensity per se but rather light wavelength (ultraviolet and other wavelengths whose representation in sunlight changes quantitatively as the sun sets).

Although the present results suggest that captive robins enter roosttime restlessness earlier on cloudy days than on sunny ones, the observed differences were small relative to the variability of the data overall. Experiment 1B, which entailed more frequent observation on a greater number of days, provided a more focused look at the effect of cloudiness on roosttime restlessness.

EXPERIMENT 1B

Method

Five of the eight robins used in Experiment 1A served as subjects. The five birds, by then 4.5 years old, were maintained under similar housing conditions as in Experiment 1A, although the present study was conducted in Lancaster, Pennsylvania, rather than New York. Perch-hop and inactivity data were collected from 2:00 p.m. to 5:30 p.m. on 5 separate days. Two of these days were completely overcast (January 7 and 8, 1979), while the remaining 3 days were blue-skied and sunny (January 3, 4, and 9). Each of the subjects was monitored by a human observer for 1 min every 10 min.

Results

Initial inspection of the results made clear that, because of individual differences in both initiation and duration of roosttime restlessness, group averaging of the data would obscure rather than clarify the findings. Consequently, the data for the 2 cloudy days were averaged for each robin individually, as were the data for the 3 sunny days (Figure 2).

The times of peak, cessation, and to a lesser extent initiation of roosttime restlessness were shifted forward 10-40 min on cloudy days for Robins 1 through 4; neither duration of the restless period nor magnitude of the peak was affected in any regular fashion by cloud cover. For the fifth subject (Robin 5), times of initiation and peak did not appear to be substantially affected by cloud cover, although time of cessation was.

The time of maximum, or peak, restlessness was derived from the inactivity data of each bird, and these peak times were averaged across all five birds. The average time of peak restlessness was 4:43 p.m. on sunny days and 4:17 p.m. on cloudy days, a difference of 26 min. When the same calculations were made on the perch-hop data, the average time of peak restlessness was 4:44 p.m. on sunny days and 4:08 p.m. on cloudy days, a difference of 36 min.

Figure 2. Seconds of inactivity (on left) and number of perch hops (on right) as a function of time of day, for each of five separate subjects (R-1 through R-5). Each bird's data represent the average of 3 sunny days and the average of 2 cloudy days, respectively.

Discussion

For most of the robins in the present study, roosttime restlessness occurred earlier on cloudy than on sunny days. This finding is consistent with the field observation of Speirs (1957) that "on clear nights the peak of the flight (to the roost) occurred well after sunset. . . . On cloudy nights, the peak occurred earlier" (p. 21). The correspondence between such observations of roosting in wild robins and the present laboratory findings offers further evidence that the high activity shown by captive robins at dusk is, in fact, a behavioral correlate of the birds' urge to travel to a communal roost site.

The present results are also consistent with the notion that an important stimulus for restlessness is the overall intensity of ambient light, although the possibility that other factors (light wavelength, endogenous rhythms) play contributory roles cannot be excluded. Previous work (Eiserer, 1980c) has indicated seasonal changes in the time of roosttime restlessness relative to sunset, with restlessness occurring relatively later (i.e., at lower light intensities) in summer than in winter. Thus, if light intensity governs the

time of restlessness on any given day, this factor appears to interact with other variables that change across time of year. Further research in which light intensity and wavelength are manipulated directly across different daily and seasonal time periods would permit more definite conclusions on these issues.

EXPERIMENT 2A

According to the available literature (which is by no means definitive), a marked shift in sociability characterizes breeding robins as a function of time of day. During the daytime, the birds are territorial and basically antagonistic towards conspecifics (Young, 1951); at dusk, however, the birds become flockers and actually seek out conspecifics at the roost site (Brewster, 1890). It is possible, therefore, that the dusk activity shown by captive robins in previous studies was the result of housing the birds under visual, but not auditory, isolation from conspecifics. Perhaps roosttime restlessness would disappear if captive robins had visual access to conspecifics, since the birds would not then be so socially deprived. Alternatively, the restlessness might have resulted from the social stimulation of the auditory exchange. In that event, roosttime restlessness might not occur in robins who were completely isolated and thus not exposed to auditory stimulation from conspecifics.

The first two studies of Experiment 2 sought to address these possibilities by determining (1) whether the daily activity pattern reported for captive robins occurs when the birds have both visual and auditory contact with one another and (2) whether the same daily pattern occurs when the birds are totally isolated.

Method

Five robins, selected at random from the eight birds described in Experiment 1A, were used. Except for the absence of cardboard dividers between the cages, the birds were maintained under the same housing conditions as in Experiment 1.

Because the cage dividers were removed and the five cages were placed along a single row, each robin was readily able to see the bird housed on either side of its cage. Visual access to less proximate neighbors was of course more restricted. Perch-hop and inactivity data were collected from 6:50 a.m. to 5:30 p.m. on January 7 and 8, 1978. Each subject was monitored by a human observer for 1 min every 10 min.

Results and Discussion

Although the robins' activity pattern (Figure 3) did not include a clear morning peak, this is not unusual for this species during the month of January (Eiserer, 1979). What the obtained pattern does make clear is that a burst of activity occurred at dusk. Roosttime restlessness, then, occurs even if captive robins have visual (as well as auditory) access to a limited number of conspecifics. Whether conspecifics are necessary for such restlessness was examined next.

Figure 3. Group mean seconds of inactivity per minute (top) and group mean number of perch hops per minute (bottom) as a function of time of day, in birds with visual-auditory access to conspecifics.

EXPERIMENT 2B

Method

Because of the great amount of experimenter time that all-day observations of individual birds entailed, the present study was restricted to two subjects (one male, one female). The birds, selected randomly from the subjects of Experiment 2A, were housed in the same cages described in Experiment 1.

The female was monitored from 6:55 a.m. to 5:35 p.m. on January 13, 1978, and the male was monitored during the same period on January 16; both days were predominantly sunny. Two days prior to each of these observation days, the appropriate bird (in its cage) was removed from the colony room in which the other robins were maintained and placed in another sun-lit room by itself. The latter room (the experimental room) was located on the side of the building opposite to the colony room. The two rooms were approximately 80 m apart, with numerous doors, rooms, and cinderblock walls interposed.

A human observer, who sat 2.5 m in front of the bird's cage, quantified each subject's behavior in terms of inactivity and perch hopping. Two experimenters took turns observing the subjects in shifts of 3-4 h duration; except for the brief periods in which one experimenter replaced the other, the subjects were monitored continuously.

Results and Discussion

The data of each subject were analyzed by deriving the mean seconds of inactivity per minute and the mean number of perch hops per minute, across time blocks of 15 min (Figure 4). Marked individual differences are apparent, with Bird 1 showing more morning activity as well as greater restlessness at dusk (i.e., earlier initiation, greater peak, and longer

Figure 4. Inactivity (on left) and perch hops (on right) as a function of time of day, for each of two birds in social isolation.

duration) than Bird 2. Nevertheless, both subjects showed clear roosttime restlessness in both response measures.

Experiments 2A and 2B have suggested that whether robins are totally isolated or are permitted visual-auditory access to several conspecifics, the birds display a daily activity pattern that includes marked restlessness at dusk. Thus, neither social stimulation nor social isolation would appear to be necessary for roosttime restlessness to occur. Whether or not these two related factors can at least affect the magnitude of restlessness was examined in Experiment 2C.

EXPERIMENT 2C

Method

Six robins were selected at random from the birds used in Experiment 1A. Each bird was observed under two conditions: *isolation*, in which an individual subject was placed by itself in the experimental room described in Experiment 2B, and *nonisolation*, in which all six subjects were placed together (although in separate cages) in the experimental room, such that each bird had visual and auditory access to conspecifics. Transfer of the birds and their cages between the experimental room and the colony room was always accomplished in the early daylight hours.

Observations were taken by a human observer during 60 sec every 10 min during the last few hours of daylight on each of 28 days in June-July 1979. During the first 12 days, each subject was individually monitored in isolation twice; on Days 13-16, all six subjects were monitored in nonisolation four times; on the last 12 days, each subject was again monitored twice in isolation. Thus, 4 days of data (both inactivity and perch hops) were collected for each bird under each experimental condition.

Results

Inactivity and perch-hop scores were calculated for each bird under each experimental condition. These scores represented the average number of seconds of inactivity per minute (or the average number of perch hops) generated by a given subject during the last hour (i.e., during the last six 1-min observation pe-

riods) before the bird settled down for the night. This mode of analysis controlled for variability in initiation of roosttime restlessness caused by either individual differences or weather conditions; moreover, 1 h is sufficiently long in most cases to encompass the entire duration of roosttime restlessness. In computing the scores for each bird, data from the 4 isolation days were averaged together, as were data from the 4 nonisolation days.

Both response measures (Figure 5) indicated that the robins were more active at dusk when isolated from conspecifics than when grouped in the same room [$t(5)=3.75$ for inactivity and 2.82 for perch hops, $p < .05$ in both cases].

Discussion

The present findings suggest that roosttime restlessness is enhanced by social isolation and/or suppressed by social stimulation. As such, the data are consistent with the notion that robins may have a "drive," or "need," to be with conspecifics during the roosting period. This suggestion must be qualified by the fact that the present data were collected during June-July, part of the birds' normal breeding season. However, given that robins are actually more gregarious during nonbreeding periods (Eiserer, 1976, pp. 151-163), the present findings probably have year-round generality.

As noted by Brewster (1890), the marked sociability of wild robins during the roosting period presents a parallel with the birds' migration period; that is, during both roosting and migration, robins abandon their characteristic territoriality and become flockers who seek the company of conspecifics. Numerous other parallels can be found between roosting and migration (Eiserer, 1979, 1980b). For example, wild robins—normally bold birds during the breeding season—become quite timid at the approach of human beings both at their roost sites and during the migration seasons. Such increased wariness, if it were also to occur in captive robins, could conceivably

Figure 5. Mean seconds of inactivity per minute (on left) and mean number of perch hops per minute (on right) during the last hour of daylight, when visual-auditory access to conspecifics was permitted (grouped) and when it was not (isolated).

underlie much of the restlessness at dusk that these birds display in the presence of human observers. Indeed, whether captive robins would show roosttime restlessness at all in the absence of a human observer was examined in Experiment 3A.

EXPERIMENT 3A

Method

Subjects included four 5-year-old robins (obtained from the Amherst area) and two 1-year-olds (from Lancaster). The former were among the subjects used in Experiments 1 and 2. The birds were individually housed in the same sort of cages and under the same general conditions described in Experiment 1.

Observations were made from a room adjacent to the robins' colony room through use of a closed-circuit television system. Each bird was monitored in terms of inactivity and perch hops for 60 sec every 10 min, from 6:00 a.m. through 6:40 p.m. on each of 2 days (March 17 and 19, 1979).

Results and Discussion

The data were analyzed by computing group means across blocks of two successive observation periods (i.e., the data for 6:00 and 6:10 a.m. were combined, etc.) and across the 2 observation days (Figure 6). Even though a human observer was not present, the robins showed the typical activity pattern, that is, a morning peak that declined across the daylight hours and then a second peak at dusk. Thus, human presence is not essential for roosttime restlessness to occur. Whether the restlessness at dusk is actually enhanced by the presence of a human observer was investigated in Experiment 3B.

Figure 6. Group mean seconds of inactivity per minute (top) and group number of perch hops per minute (bottom) as a function of time of day, when a human observer was not visible.

EXPERIMENT 3B

Method

The birds and the housing conditions were the same as those described in Experiment 3A. Each robin was monitored for 60 sec every 6 min from 5:00 p.m. through 8:30 p.m. on each of 8 days (August 13-20, 1979). On 4 of these days (August 13, 15, 17, 19), the subjects were observed from an adjacent room through closed-circuit television; on the other 4 days, an observer sat quietly in the colony room, about 2 m in front of the birds. Both inactivity and perch hops were recorded.

Results

Single inactivity and perch-hop scores were calculated for each bird under both experimental conditions, with each score representing the average seconds of inactivity per minute (or the average number of perch hops) generated by a given subject during the last hour before the bird settled down for the night. In computing the scores for each bird, data from the four observer-present days were averaged together, as were data for the four observer-absent days.

Both response measures indicated that the robins were more restless at dusk when the observer was present visibly than when observations were made from an adjacent room (Figure 7). *t* tests for related measures revealed that the difference was significant for inactivity [$t(5) = 4.48$, $p < .05$] and marginally significant for perch hops [$t(5) = 2.48$, $p < .06$].

Discussion

While not dependent upon human presence for its occurrence (Experiment 3A), roosttime restlessness is nevertheless affected by such presence. Although Experiment 3B does not identify the process that underlies increased restlessness in the presence of a human observer, it seems reasonable to suggest that "fear of humans" is the mediating factor. Gallup and Suarez (1980) have reported that chickens react to human presence much as they would to a predatory encounter; the captive but untamed robins used in the present research may have done likewise. The results of Experiment 3, then, join those of Experiment 2 in implying a degree of wariness (fear of human beings) and sociability in robins at dusk that might not be expected from the bold, mutually antagonistic nature that characterizes these birds at other periods (Eiserer, 1976).

EXPERIMENT 4A

All previous research on roosttime restlessness in captive American robins (Eiserer, 1979, 1980a, 1980c, 1980d; Palmer, 1970) has examined birds in cages so small that little locomotor activity other than perch hops was permitted. The question thus arises of whether the restlessness is partly an artifact of the

Figure 7. Mean seconds of inactivity per minute (on left) and mean number of perch hops per minute (on right) during the last hour of daylight, in both the absence and the presence of a human observer.

unnatural restriction of such a highly mobile organism. Although Brewster's (1890) mention of restlessness in free-living robins argues against this possibility, direct evidence involving captive birds is needed. The present study assessed the activity pattern of robins in a large flight cage in order to determine whether the birds—no longer confined to mere hopping—would still become restless at dusk.

Method

Subjects. Six of the birds used in Experiment 1, now 6 years old, were housed in a single, rectangular flight cage ($1.2 \times 1.8 \times 4.3$ m). This enclosure provided approximately 140 times the space afforded by the cages in Experiments 1-3.

Within the flight cage were three "trees," each of which provided a set of 11 parallel perches that extended across the width of the cage at heights ranging from 15 to 115 cm above the ground. One tree was located at either end of the cage, while the third was in the middle.

Mynah bird pellets and water were available continuously in bowls placed on the floor, which was covered with a carpet of green, synthetic "turf." The cage itself was located in a room that had windows on three sides. Sunlight passing through these windows provided the only illumination for the cage.

Procedure. Observations were taken on June 15 and 16, 1980, several weeks after the robins had first been placed in the flight cage. Activity was assessed in terms of *flight responses*, in which a bird either (1) moved from one tree to another or (2) moved from a tree to the floor, or vice versa. Lateral movements along a single perch, movements from one perch to another within a single tree, and movements along the cage floor were not monitored.

Although each bird wore an individually colored leg band, the fine-mesh screen of the cage prevented the experimenter from reliably discriminating these bands from the observation position, about 2.5 m away. Consequently, flight responses were not recorded on an individual basis but only for the group of subjects as a whole. Specifically, total number of flights were recorded for each 5-min interval from 6:00 a.m. to 9:00 p.m.

Results and Discussion

The data were analyzed by computing the average number of flights per 5-min interval across 30-min blocks of time, and across both days of observation. Thus, the first data point in Figure 8 indicates that, on average, each bird made 2.7 flights during each

5-min interval from 6:00 to 6:30 a.m. As the figure makes clear, the robins showed the typical (though highly variable) morning activity peak and the typical decline in activity across the afternoon hours. They did not, however, show an activity peak at dusk. These flight data were representative of the robins' locomotor behavior more generally, because at dusk the birds did not engage in great amounts of floor-running or any other locomotor behavior.

These unexpected results, which represent the first clear demonstration of a lack of roosttime restlessness in robins maintained under natural illumination, could have been caused by either of two factors. First, as suggested earlier, roosttime restlessness may be a laboratory phenomenon that appears only when birds are housed in very small cages. Alternatively, restlessness may have been suppressed in the present study by the group housing. These two possibilities were further examined in Experiment 4B.

EXPERIMENT 4B

Method

Five of the six robins from Experiment 4A served as subjects. Flight responses were monitored under two experimental conditions: *isolated*, in which a single subject was alone in the flight cage while the other four subjects were kept in another room, and *grouped*, in which all five birds were together in the flight cage. The occurrence of roosttime restlessness in the isolated condition but not the grouped condition would eliminate cage size as an explanation for the results of Experiment 4A and implicate the presence of conspecifics as the crucial factor.

Each bird was observed twice under each condition over a 12-day period (October 8-19, 1980). On the first day, all five birds were observed as a group; on the next 10 days, each bird was observed twice in isolation; and on the 12th day, the birds were observed as a group again. Transfer of birds in and out of the flight cage occurred in the early morning, and flight responses were monitored during approximately the last 3 h of daylight on each day.

Results and Discussion

Variability in weather conditions (i.e., cloudiness) across the course of the study prevented analysis of

Figure 8. Mean number of flight responses per 5-min interval as a function of time of day, for robins housed together in a large cage.

Figure 9. Mean number of flight responses per 5-min interval relative to time of retiring, when robins were either grouped together or isolated in a large cage.

the "isolated" data in terms of absolute time (i.e., time of day). Instead, the data were analyzed in terms of "minutes before retiring," where retiring was defined as the beginning of three consecutive 5-min intervals in which no flight responses were emitted by either the isolated bird or the group of birds as a whole. Figure 9, then, shows the average number of flights per 5-min interval across 10-min blocks, relative to time of retiring. When the robins were isolated, a burst of flight responses immediately preceded their settling down for the night. In contrast, no increase in flight responses occurred at dusk when the five subjects were grouped together.

In this study, the "grouped" data were somewhat misleading because one or two birds showed increased wing-flicking as well as lateral movements along single perches at dusk. The fact that these signs of restlessness seldom culminated in flight behavior in the grouped condition (Figure 9) indicates strong—albeit incomplete—suppression of roosttime restlessness. Perhaps the reduced number of birds in the present study (five, instead of the six in Experiment 4A) accounted for the incomplete suppression of restlessness.

The present findings, in any event, have a number of important implications. First, roosttime restlessness appears not to be a mere artifact of small cages. This conclusion, in turn, further supports the notion that the restlessness of captive birds at dusk is comparable to the restlessness that field workers have observed in free-living robins.

Second, the present results both replicate and extend the finding of Experiment 2C that stimulation from conspecifics can suppress roosttime restlessness. When visual-auditory access to a number of conspecifics is complete (i.e., the birds are not maintained in separate cages), virtually no restlessness occurs at all.

Finally, the present results suggest a fundamental reinterpretation of roosttime restlessness. Rather than simply being an "urge to travel" to the roost site, the restlessness apparently in part reflects an

"urge to be with conspecifics." In the natural setting during the breeding season, these two factors go hand in hand, since territorial robins must travel to a common meeting place in order to be with conspecifics. Under the present laboratory conditions, in which birds were maintained in a small flock such that traveling to a communal roost site was unnecessary, restlessness at dusk was almost completely absent. The urge to be with conspecifics cannot be the only cause of roosttime restlessness, however, since in winter most robins spend the entire day with flocks of conspecifics, and yet still travel some distance to communal roost sites at dusk (Black, 1932; Widmann, 1895).

GENERAL DISCUSSION

The present work indicates that roosttime restlessness is a robust characteristic of the behavior of American robins in captivity. It occurs regardless of the presence or absence of cloud cover, in both the presence and the absence of conspecifics or a human observer, and in large as well as small cages. At the same time, the phenomenon is malleable under the influences of ambient illumination (Experiment 1), stimulation arising from conspecifics (Experiments 2 and 4) and human beings (Experiment 3), and variables associated with incubation (Eiserer, 1980d) and time of year (Eiserer, 1980c). Of course, much more remains to be studied about each of these and their interactions. (Can artificial decreases in illumination initiate roosttime restlessness? What is the nature of the stimulation from conspecifics that suppresses restlessness?)

More generally, the American robin would seem an ideal species for the laboratory analysis of communal roosting in birds, a phenomenon replete with scientific mystery and challenge. For example, given the significant energy expenditure that commuting to a roost involves, the habit must surely offer high survival value for the many species that display it. Yet, the exact nature of this value (or values) remains obscure.

An obvious possibility is protection from predators, but despite the fact that robins usually select densely vegetated areas for their roosts, they may actually be no safer there than they would be at their nest areas. Scattered among their respective territories, the birds could never suffer concentrated predation at night; gathered densely in a communal roost, however, they may be killed in greater numbers by predators (e.g., bobcats) that are attracted to the site (Black, 1932). Of course, the risk of predation for any individual bird might still be less at the roost than when sleeping solitarily (Counsilman, 1974), but there is no evidence that this is true for robins.

A second possible benefit of communal roosting, particularly during the breeding season and early fall,

might be the preparation it affords young robins for the southern migration. The daily flights to and from the roost may provide helpful practice in navigating over at least short distances (Chapman, 1916). Relatedly, the experience may be an important prerequisite for *Ortsruhe* (or *Ortstreu*), that is, the tendency of robins to return the following spring to the locality where they hatched (as many as 90% of all robins may migrate back to within 25 miles of their hatchplace; Farner, 1945). *Ortsruhe* is itself advantageous because it helps ensure that the younger generation will settle in ecological regions where the species has successfully propagated (as proved by the birds' parents).

Communal roosting may also permit increased efficiency in finding food, in that individuals who have had limited foraging success on one day may thereafter follow roostmates to better feeding areas (Ward, 1965). Although robins do occasionally forage communally during the breeding season, most food at this time is obtained within their individual territories. Roost-related feeding efficiency could perhaps be important for robins during the fall and winter when they feed more regularly in flocks.

Still another possible benefit stems from the ideas of Wynne-Edwards (1962). Although these ideas have been attacked for depending upon the questionable mechanism of group selection (e.g., Wiens, 1966), the basic concept of "epideictic displays" (behaviors specifically adapted to provide an immediate local census; Barash, 1977, p. 71) can be utilized without requiring group selection. In particular, if most robins within a given area convene regularly at one place, the potential exists for what, in effect, is a local census which could be instrumental in self-regulation of the robin population. In most sectors of North America, robins normally rear two or three broods of young each season. After breeding activities are completed, the birds abandon their territories and spend much time building up body fat (primarily by eating great quantities of wild berries) before the fall migration. Perhaps during those seasons when population pressures are great, individual pairs of robins who rear only one or two broods gain a valuable headstart in exploiting limited berry resources and are thus better able to meet the demanding rigors of migration.

This census hypothesis seems less relevant to the roosting behavior that robins show during nonbreeding periods, such as when they are wintering in the South. Another potential advantage of communal roosting lies in the conservation of body heat that sometimes accrues from sleeping in crowded quarters. Unfortunately, research has found only slight thermoregulatory benefits from communal roosting (e.g., Walsberg & King, 1980), and this possibility remains speculative. Thus, future laboratory analysis (e.g., on antipredator reactions of roosting robins, effects

of temperature on the roosting tendency, etc.) has potentially much to contribute to our eventual understanding of this fascinating area of bird behavior.

REFERENCES

- BARASH, D. P. *Sociobiology and behavior*. New York: Elsevier North-Holland, 1977.
- BLACK, J. D. A winter robin roost in Arkansas. *Wilson Bulletin*, 1932, **44**, 13-19.
- BREWSTER, W. Summer robin roosts. *Auk*, 1890, **7**, 360-373.
- CHAPMAN, F. M. *The travels of birds*. New York: Appleton, 1916.
- COUNSILMAN, J. J. Waking and roosting behaviour of the Indian Myna. *Emu*, 1974, **74**, 135-148.
- EISERER, L. A. *The American Robin: A backyard institution*. Chicago: Nelson-Hall, 1976.
- EISERER, L. A. Roosttime restlessness in captive American Robins. *Animal Learning & Behavior*, 1979, **7**, 406-412.
- EISERER, L. A. Ontogeny of roosttime restlessness in American Robins. *Auk*, 1980, **97**, 194-196. (a)
- EISERER, L. A. Roosting behavior of the American Robin. *Pas-senger Pigeon*, 1980, **42**, 96-101. (b)
- EISERER, L. A. Seasonal changes in times of awakening, retiring, and roosttime restlessness in captive American Robins. *Psychological Record*, 1980, **30**, 277-281. (c)
- EISERER, L. A. Suppression of roosttime restlessness in incubating American Robins. *Bird Behaviour*, 1980, **2**, 107-111. (d)
- EYSTER, M. B. Quantitative measurement of the influence of photoperiod, temperature, and season on the activity of captive songbirds. *Ecological Monographs*, 1954, **24**, 1-28.
- FARNER, D. S. The return of robins to their birthplaces. *Bird-Banding*, 1945, **16**, 81-99.
- GALLUP, G. G., JR., & SUAREZ, S. D. An ethological analysis of open-field behaviour in chickens. *Animal Behaviour*, 1980, **28**, 368-378.
- HOWELL, J. C. Spring roosts of the robin. *Wilson Bulletin*, 1940, **52**, 19-23.
- MEANLEY, B. The roosting behavior of the red-winged blackbird in the southern United States. *Wilson Bulletin*, 1965, **77**, 217-228.
- PALMER, J. D. The biological clock of birds. In *Field studies in natural history*. New York: Van Nostrand Reinhold, 1970.
- PALMGREN, P. On the diurnal rhythm of activity and rest in birds. *Ibis*, 1949, **91**, 561-576.
- SEIBERT, H. C. Light intensity and the roosting flight of herons in New Jersey. *Auk*, 1951, **68**, 63-79.
- SMITH, R. W., BROWN, I. L., & MEWALDT, L. R. Annual activity patterns of caged non-migratory white-crowned sparrows. *Wilson Bulletin*, 1969, **81**, 419-440.
- SPEIRS, J. M. Robin roosts. *Federation of Ontario Naturalists Bulletin*, 1957, **76**, 18-23.
- TORREY, B. Robin roosts. *Atlantic Monthly*, 1890, **66**, 492-498.
- WALSBERG, G. E., & KING, J. R. The thermoregulatory significance of the winter roost-sites selected by robins in Eastern Washington. *Wilson Bulletin*, 1980, **92**, 33-39.
- WARD, P. Feeding ecology of the Black-faced Dioch. *Ibis*, 1965, **107**, 173-214.
- WIDMANN, O. A winter robin roost in Missouri. *Auk*, 1895, **12**, 1-11.
- WIENS, J. A. On group selection and Wynne-Edwards' hypothesis. *American Scientist*, 1966, **54**, 273-287.
- WING, L. W. *Natural history of birds: A guide to ornithology*. New York: Ronald Press, 1956.
- WYNNE-EDWARDS, V. C. *Animal dispersion and its relation to social behaviour*. New York: Hafner, 1962.
- YOUNG, H. Territorial behavior in the eastern robin. *Proceedings of the Linnaean Society of New York*, 1951, **58-62**, 1-37.