SUPPRESSION OF AUTUMNAL MIGRATORY UNREST IN DARK-EYED JUNCOS HELD DURING SUMMER ON, NEAR, OR FAR FROM THEIR PREVIOUS WINTERING SITES

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ABSTRACT.—In previous experiments, Dark-eyed Juncos (*Junco hyemalis*) were captured on a winter home range to which they had shown year-to-year site fidelity and held there until just before the autumn. They failed to show normal autumn migratory restlessness and fattening, which suggested that previous experience at the migratory destination suppressed readiness to migrate. We asked what the suppressing cues might be. Possibilities included very local features peculiar to the individual's winter home range (e.g. its trees) and cues common to the general region (e.g. geophysical or celestial information); features of the latter sort might give information about latitude. To test these possibilities we monitored autumn restlessness and fattening of new groups of juncos that were held before migration where some could perceive landmarks of their familiar winter home range and others only more general information about their location. In autumn those held at, near, and far south of their winter home ranges again failed to become restless or fat. A small group held far north of their winter home ranges became somewhat restless, significantly more so than the others. These may have perceived that they had not reached their usual winter latitude, but alternative explanations are possible. *Received 25 June 1986, accepted 12 December 1986.*

IN some bird species the onset and termination of migratory behavior appears to be controlled largely by an endogenous circannual mechanism. Deprived of potentially important environmental timing cues such as change in day length, weather, food availability, etc., captive individuals nevertheless enter a state of readiness to migrate (become fat and restless) whose timing corresponds approximately to the migration season of free-living members of their species (Gwinner 1968a, b, 1972; Berthold 1984) or population (Berthold and Querner 1981, Berthold 1984). In other species seasonally changing environmental information drives the annual cycle. Under constant conditions, such birds may fail to enter the migratory state (Moore et al. 1982, Donham et al. 1983). It seems likely that in an adult bird previous migratory experience interacts with an underlying calendar-like mechanism of either type to modify aspects of the timing of migration. For example, if an individual returns to its breeding or nonbreeding site of a previous year and passes out of the migratory state as a consequence, experience may have prolonged its migratory condition to let it reach its destination, then have terminated the condition to let it settle there. Until recently there has been

almost no support for this role of experience (Gwinner 1986). In the only relevant experiment we know of other than those described herein, spring exposure of *Sylvia borin* and *S. atricapilla* to sites at which they had been held for a period after hatching did not suppress their migratory restlessness (Gwinner and Czechlik 1978). In adult Dark-eyed Juncos (*Junco hyemalis*), however, experimental evidence (Ketterson and Nolan 1983a, in press a) has indicated that perception before the migration season of the destination of the preceding year's autumn migration has more than a modifying effect on termination of the migratory state; apparently, the state is suppressed altogether.

Initially we found (Ketterson and Nolan 1983a) that juncos faithful to a winter home range at Bloomington, Indiana, when held there during spring and summer, failed to become restless (show *Zugunruhe*) and deposit migratory fat during autumn. Control groups of juncos monitored simultaneously but caught in Canada in summer and brought to Bloomington, which almost certainly was not their winter home range, fattened and became restless. Suppression was repeated in a second experiment on a new group of site-faithfuls (Ketterson and Nolan in press a) in which Canada-

caught birds that had been held for more than a year nevertheless became restless and fat. This result eliminated long captivity, failure to migrate in spring, residence in the winter range during summer, and failure to breed as likely causes of the suppressed autumnal state. The most probable explanation that remained was that before autumn the Indiana site-faithful birds had perceived and responded to some feature of their migratory destination, which caused them not to become migratory. The experiment reported here was designed to identify the suppressing cues. During spring and summer we exposed groups of juncos to different potential sources of information about their present locations relative to the locations of their winter home range and observed which group(s) failed to become restless and fat in autumn.

It is not possible to trace a junco from its summer site to its winter site. Therefore, we could not take the direct approach of catching individuals on their breeding home range in late summer, transporting some to their familiar winter home range, transporting others to unfamiliar sites, and then comparing the autumn restlessness and fattening of the two groups. Instead, in winter we captured individuals at a series of locations we knew each had used in the previous winter (because we had banded it there) and held them outdoors at a single location from the time of capture until the following autumn. For some the single location (an aviary on the Indiana University campus) was their familiar winter home range, for others it was near the winter home range, and for still others it was far (>300 km) to the north or south of the winter home range.

We made several predictions. First, if suppression requires perception of cues highly specific to the winter home range, e.g. certain trees or topographic landmarks, juncos faithful to sites other than the aviary would show no autumn suppression. Second, if the cues are regional, e.g. star patterns, odors, or the geomagnetic field, juncos from the aviary and other winter sites in the Bloomington region would show suppression, but juncos from distant winter locations would not. Finally, as a variant of the second prediction, if the cues are regional and have their effect because they give information about latitude, juncos from distant locations north of Bloomington might behave dif-

ferently than juncos from far south of it. Southern juncos might be more likely to become migratory if they perceived that the holding site was not far enough into the winter range, while northern juncos might be less likely to become migratory because migration would move them northward for the winter.

METHODS

Origin and treatment of subjects.—Migratory juncos breed largely in Canada and winter in southern Canada and most of the United States, where winter populations settle by about 1 December (Ketterson and Nolan 1976, 1985). Independent estimates agree that annual survivorship of adults is about 50% (Ketterson and Nolan 1982, 1985). Many fewer than 50% of juncos banded at a wintering site return there in the following year (unpubl. data); therefore, in any winter not all surviving individuals exhibit fidelity. Of banded juncos that do return to the same home range for a second winter, about 50% return for a third, about 50% of these for a fourth, etc. (Ketterson and Nolan 1985). Therefore, if we catch an individual at the same location in two successive winters, we can predict with considerable confidence that this location will be the destination of its autumn migrations for the rest of its life.

The experimental subjects formed four groups. Group 1 consisted of 9 males and 2 females from the grounds of the Bloomington aviary; Group 2 of 6 males and 1 female from three locations 10–18 km from the aviary; Group 3 of 6 males from Kalamazoo, Michigan, about 350 km north of the aviary; and Group 4 of 2 females, one each from Clemson, South Carolina, and Nashville, Tennessee, about 700 km southeast and 350 km south, respectively, of the aviary. (Group 4 originally consisted of 9 birds, but 7 escaped before the experiment.) All subjects had been banded in a winter before the winter of 1981–1982, when they were recaptured at the original banding sites and, for Groups 2 and 3, taken by automobile to Bloomington. All capture sites were south of the breeding range; hence, all subjects had migrated northward in the spring after they were banded and had returned to their wintering sites during autumn 1981.

After capture, groups were intermingled in large outdoor aviary cages (for details see Ketterson and Nolan 1983a). From 18 August 1982 until late December, except as noted below, birds lived in individual registration (activity) cages on a rooftop 1.5 km from the aviary. Therefore, no bird was on its winter home range during monitoring. In the one exception, between 6 October and 9 October all were returned to the large aviary cages and allowed to exercise together. The birds were caged together at the aviary
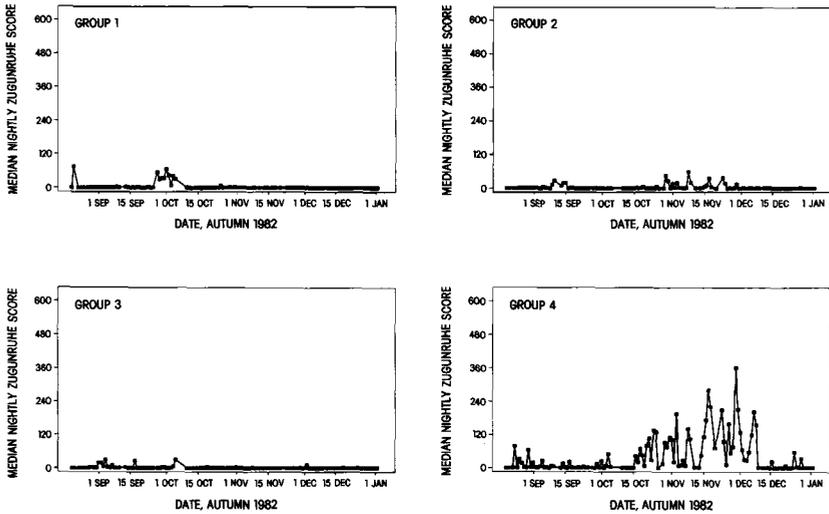
Fig. 1.   Median nightly autumn *Zugunruhe* score according to group. For a description of the groups, see Methods.

from late December 1982 until 28 February 1983, when they were returned to the rooftop cages and monitored until 1 June 1983.

Zugunruhe.—As in earlier experiments (e.g. Ketterson and Nolan 1983a), measures (hereafter, scores) of *Zugunruhe* were (1) the number of 30-s intervals during which an individual hopped on or off its perch at least once between 2100 and 0430 (its nightly score, maximum possible = 900), (2) the sum of its nightly scores during the season (its seasonal score), (3) its highest nightly score (maximum night), and (4) the number of nights it was active during at least 30 min (i.e. nightly score ≥ 60, an active night).

We monitored no Canada-caught juncos in 1982, but in retrospect it is clear that results presented below can be better evaluated when compared with data produced by juncos caught in summer in Canada and monitored a few weeks later in Indiana. Therefore, we refer to data produced by several different sets of Canada-caught juncos in other years (Ketterson and Nolan 1983a, 1985, in press a, b), but we make no statistical comparisons across years because of annual differences in weather.

Female juncos, which on average winter south of males (Ketterson and Nolan 1976, 1983b, 1985), exhibit a weak tendency to become more restless than males in autumn (Ketterson and Nolan 1985). Because sexual composition of groups varied, we return to this point below.

Body mass.—Change in body mass and visible fat class in juncos represents variation in extractable fat (Rogers, Ketterson, and Nolan in prep.). Birds were weighed at the beginning of monitoring and approximately biweekly thereafter, always in midafter-

noon. Visible subcutaneous fat deposits were scored on a scale of 0–5, as described previously (Nolan and Ketterson 1983). All birds were in class 0 when the experiment began. Males tend to be larger than females, and therefore we compare body mass of individuals in terms of change during the experiment. We report change as the absolute difference between mass at the start of the experiment and maximum mass attained thereafter and the maximum percentage deviation from initial mass. Free-living juncos are lean after arriving from migration, and depending on their winter latitude they fatten during winter (Nolan and Ketterson 1983). To avoid this winter effect we restricted analysis of body mass to measurements before 1 December.

Molt.—Each time a bird was weighed, its molt was examined until postnuptial molt was complete. Progress was evaluated as in other experiments (Ketterson and Nolan in press a).

Statistical analyses.—Analysis of *Zugunruhe* and fattening was by rank-order statistics, with individuals pooled across groups and low values assigned to low ranks. Statistical computations were done on an IBM PC employing a statistical software package (Microstat by Ecosoft). Probabilities are one-tailed unless otherwise stated and are considered significant when ≤ 0.05.

RESULTS

Autumn Zugunruhe.—The median nightly scores of each group in autumn 1982 are shown in Fig. 1. This figure is to be compared with
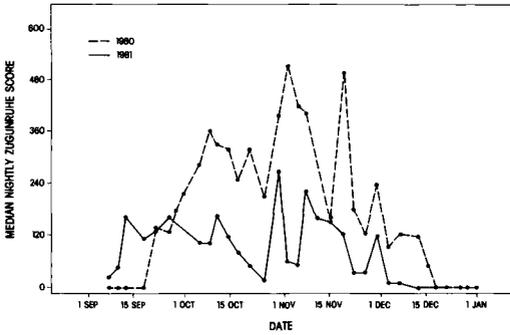
Fig. 2. Median nightly (2 nights/week) autumn *Zugunruhe* score of 10 juncos caught in Canada in July 1980; monitored at Bloomington, Indiana, during autumn 1980; held outdoors there until autumn 1981; and then monitored again. (Reprinted from *Animal Behaviour*, 1987.)

Fig. 2, which depicts the median nightly score of a group of 10 adult juncos that were caught on their Canadian breeding ground in late summer 1980, driven to Bloomington, and monitored there in the autumns of 1980 and 1981. The restlessness of the Canada-caught juncos in 1980 was typical of that shown by other groups with similar histories (e.g. Ketterson and Nolan 1983a: fig. 1, 1985: fig. 5b, in press b). The level declined in 1981, presumably the effect of 14 months of captivity. No group in the present experiment was as active as the Canada birds in 1980, but the restlessness of Group 4 was comparable to that of the Canada birds in 1981. Groups 1–3 fell far below even this 1981 level and were essentially inactive.

To test our first prediction, that migratory readiness is suppressed only by perception of cues peculiar to a single home range, we compared Group 1 with Group 2 and also with Groups 2–4 combined (Table 1). In Wilcoxon rank-sum tests of differences between Group 1 and Group 2, results were nonsignificant (seasonal score: $z = -1.13$, $P = 0.129$; number of active nights: $z = -1.31$, $P = 0.095$; maximum nightly score: $z = -0.45$, $P = 0.325$). In comparisons of Group 1 with all other groups combined, outcomes were again nonsignificant (seasonal score: $z = -1.17$, $P = 0.122$; number of active nights: $z = -1.48$, $P = 0.070$; maximum nightly score: $z = -0.57$, $P = 0.284$).

To test the second prediction, that the suppressing cues are characteristic of a geographic region such as south-central Indiana, we compared Groups 1 and 2 combined with Groups 3

TABLE 1. Autumn *Zugunruhe*[a] of groups[b] of winter-site-faithful juncos from four locations. Values are medians, with extremes in parentheses.

	Seasonal total[c]	Maximum night[c]	Active nights[c,d]
Group 1 (n = 11)	942 (40–5,060)	145 (22–543)	4 (0–20)
Group 2 (n = 7)	1,425 (41–8,601)	158 (6–573)	9 (0–26)
Group 3 (n = 6)	1,005 (24–12,785)	160.5 (7–400)	6 (0–69)
Group 4 (n = 2)	4,876 (3,895–5,858)	376 (294–459)	26 (23–28)

[a] Perch hops were monitored by microcomputer during 30-s intervals between 2100 and 0430 (900 intervals/night), 18 August–late December 1982. The sum of an individual's nightly scores is its seasonal score; nights with nightly scores ≥60 are active nights.

[b] Groups defined as in the Methods.

[c] Results of most statistical tests are described in the text. Kruskal-Wallis one-way ANOVAs comparing all four groups were not significant (seasonal total: $H = 4.20$, df = 3, $P = 0.24$; maximum night: $H = 2.58$, df = 3, $P = 0.469$; active nights: $H = 5.33$, df = 3, $P = 0.149$).

[d] Ranks of individuals, with all groups pooled and smallest number of active nights ranked lowest, follow. Group 1: 3, 3, 7, 7, 10, 10, 12, 13.5, 13.5, 20, 21; Group 2: 3, 10, 15.5, 15.5, 18, 19, 24; Group 3: 3, 3, 7, 17, 22, 26; Group 4: 23, 25.

and 4 combined. Again, no probability approached significance (seasonal total: $z = -0.72$, $P = 0.235$; number of active nights: $z = -1.00$, $P = 0.159$; maximum nightly score: $z = -0.44$, $P = 0.328$).

Finally, we tested the third prediction, that juncos perceive latitude and when north of their accustomed winter home range become restless in autumn but not when at or south of that latitude, by a comparison of Group 4 with all other groups pooled and with Group 3 alone. Some differences were significant, with Group 4 tending to be more active (Group 4 vs. all groups: seasonal score, $z = -1.83$, $P = 0.034$; active nights score, $z = -2.02$, $P = 0.022$; maximum nightly score, $z = -1.54$, $P = 0.062$. Group 4 vs. Group 3: for all three comparisons, $z = -1.33$, $P = 0.091$). We repeat, however, that Group 4 consisted only of two females and that females are slightly more restless than males, on average.

Body mass and fat class.—Intergroup comparisons of mass were performed as described for *Zugunruhe*. There were some significant differences (Groups 1 and 2 combined gained more in mass than Groups 3 and 4), but the pattern did not match that suggested by the *Zugunruhe* scores (Table 2, Fig. 3). That is, the most restless group, Group 4, gained somewhat more mass
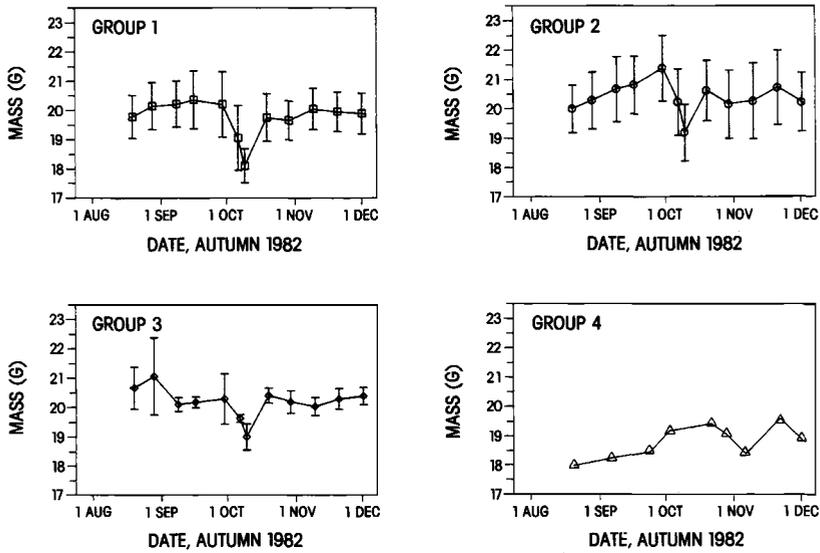
Fig. 3. Mean body mass (±2 SE) according to date and group. For a description of the groups, see Methods. Group 4 had only 2 members, and no error bars were plotted.

than the other groups pooled, but not significantly so (absolute amount: $z = -0.96, P = 0.168$; percentage change: $z = -1.01, P = 0.156$). As with Zugunruhe, no site-faithful group became as fat as juncos caught in Canada and transported to the winter range (see Ketterson and Nolan 1983a, 1985, in press a). Canada-caught birds typically increase mass by 2–3 g, i.e. 20% of their initial mass, and this is true even after they have spent a year in captivity (Ketterson and Nolan in press a).

Exercise, group living, or both, affected mass when the juncos were transferred from individual cages to large flight cages (Fig. 3). All birds lost mass during their four days together but quickly returned to pre-exercise mass when reintroduced into individual cages. This implies that all groups regulated body mass while in their individual cages, but at a lower level than Canada-caught juncos. On two other occasions we have observed the same response by juncos given this exercise opportunity.

The median fat class of all four groups (data not shown) remained below 1 throughout autumn, whereas in Canada-caught juncos the median rose to about 4, even after prolonged captivity (Ketterson and Nolan 1983a, 1985, in press a, b).

Molt.—Molt was normal and did not differ among groups. Individuals that entered molt earlier than others tended to complete it ear-

lier, and there was no correlation between the date of an individual's molt and any measure of its Zugunruhe (Spearman's rank correlation, data not shown).

Spring Zugunruhe.—Finally, whatever it is that suppresses autumn restlessness, the effect is not permanent (Fig. 4). As in previous cases of autumn suppression (Ketterson and Nolan 1983a, in press a), the activity of all groups was great and indistinguishable statistically throughout spring (Kruskal-Wallis one-way analysis of variance; seasonal total: $H = 3.18$,

TABLE 2. Maximum gain in body mass of winter-site-faithful juncos, autumn 1982, by group.[a] Values are means, with extremes in parentheses.

	Absolute gain (g)[b]	Gain as % of initial mass[b]
Group 1	1.43	5.53
($n = 11$)	(−0.8–4.1)	(−4–20)
Group 2	1.61	8.14
($n = 7$)	(0.9–3.6)	(4–17)
Group 3	0.20	1.17
($n = 6$)	(−1.3–1.1)	(−6–6)
Group 4	1.60	8.50
($n = 2$)	(1.2–2.0)	(6–11)

[a] Groups defined as in the Methods.
[b] For each individual, mass at the beginning of the experiment was subtracted from maximum mass attained thereafter before 1 December. In a Kruskal-Wallis one-way analysis of variance of absolute change, $H = 8.39$, df = 3, $P = 0.039$. In the same test of percentage change, $H = 7.11$, df = 3, $P = 0.068$.
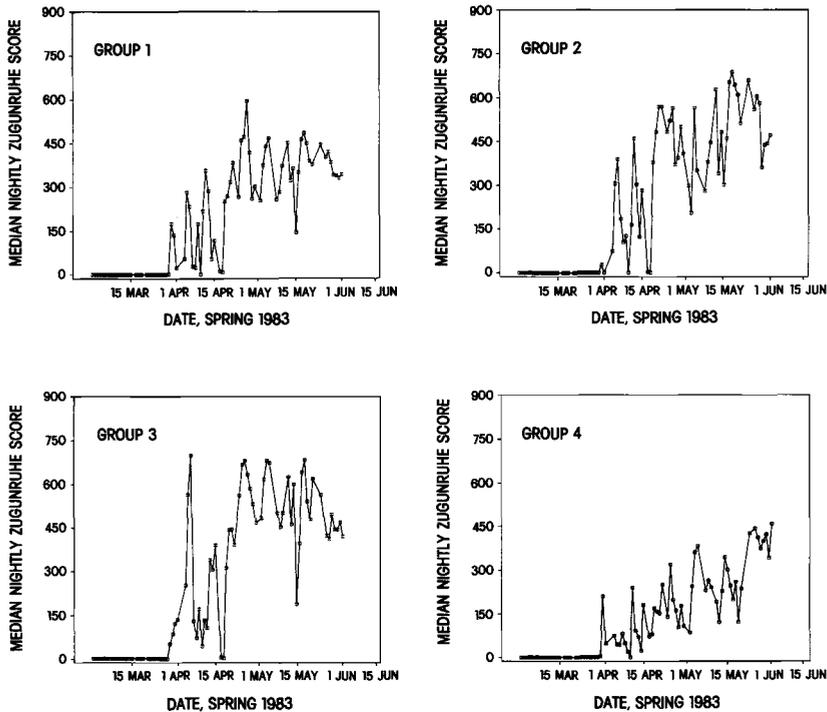
Fig. 4.   Median nightly spring *Zugunruhe* score according to date and group. For a description of the groups, see Methods.

df = 3, P = 0.365; active nights: H = 0.57, df = 3, P = 0.903; maximum nightly score: H = 2.77, df = 3, P = 0.428). All grew very fat (data not shown).

DISCUSSION

No group of winter-site-faithful juncos, regardless of capture site, became as restless and fat as birds monitored after recent capture in Canada. None of our predictions received strong support. The significantly greater *Zugunruhe* and slightly greater fattening of the two southern juncos (Group 4) that were tested north of their winter sites could support the hypothesis that cues leading to suppression of the migratory state are latitudinal, but Group 4 was too small to inspire confidence in this conclusion. Furthermore, the result might be explained in two alternative ways. First, the sample consisted of females, and gender might account for the greater restlessness. Evidence against this argument, however, is that the ranks of the *Zugunruhe* of the Group 4 females were much higher than the ranks of the other

females in the experiment. For example, in number of active nights among the 26 juncos, 2 Group 1 females ranked 7 and 13.5, the Group 2 female ranked 10, and the Group 4 females were highly active, ranking 23 and 25 (Table 1). Another distinguishing attribute of the members of Group 4 was that they were the only birds that experienced *northward* movement after capture. Groups 1 and 2 were held where captured, and Group 3 birds were moved southward. Possibly, an individual must leave its winter home range and move toward the breeding range before it can enter a state of readiness to return to the winter site. This possibility is under investigation.

If *Zugunruhe* was not fully suppressed in Group 4, there still remains the question of why the other three groups behaved differently in autumn than birds caught on the breeding range. One possibility, consistent with the fact that the annual return rate to wintering sites is below the annual survival rate, is that some individuals may never return to the winter site of an earlier year. If there are two types of juncos, those that show year-to-year site fidelity in

winter and those that do not, regulation of migration may differ between the two types. Perhaps only the non-site-faithful birds will exhibit restlessness and fatten when caged. This seems unlikely, however, because such a difference would exist only in autumn. Spring *Zugunruhe* and fattening of site-faithful juncos in this (Fig. 4) and other experiments (Ketterson and Nolan 1983a, in press a) were as great as those of juncos caught in Canada.

A second possible explanation for the suppression in Groups 1–3 and in previous experimental groups may be photoperiodic, as we have suggested before (Ketterson and Nolan 1983a, in press a). Summer days in Indiana may not be long enough to elicit autumn physiology in juncos that winter in Michigan and Indiana (compare with *Zonotrichia leucophrys*; Moore et al. 1982). Thus, when they experience Indiana day lengths shorter than the day lengths in the breeding range, they behave abnormally in autumn. In contrast, after being held in Indiana throughout winter, and therefore on day lengths normal for them at that season, spring migratory readiness is normal (compare with *Ficedula hypoleuca*; Gwinner 1986). How can this argument be reconciled with the fact that Canada-caught birds became restless in autumn even after a year in captivity in Indiana (Fig. 2)? In all our experiments, Canada-caught birds were taken at breeding sites near Wawa, Ontario, at 49°N latitude. If Indiana and Michigan juncos that have shown autumn suppression in this and earlier experiments were from breeding latitudes so far north that only summer days longer than those of Bloomington, Indiana (39°), could trigger the autumn state, this might account for our results.

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The **annual meeting of the Raptor Research Foundation** will be held **28–31 October 1987** in Boise, Idaho. For information contact **R. Howard, Chairperson, U.S. Fish and Wildlife Service, 4696 Overland Road, Room 576, Boise, Idaho 83705.**

The **11th Annual Meeting of the Colonial Waterbird Society** will be held at the Red Oak Inn in Thunder Bay, Ontario, **10–13 September 1987.** Lynn Hauta and John P. Ryder are in charge of local arrangements. Announcements of the schedule and a call for papers will be mailed to members at a later date.

The **Western Raptor Management Symposium and Workshop,** coorganized by the National Wildlife Federation and Idaho chapter of The Wildlife Society, will be held **26–28 October 1987** in Boise, Idaho. The symposium will feature technical paper sessions on the status of western raptors and their habitats, land-use activities affecting raptors, workshops, and a poster session. For information contact the **National Wildlife Federation, Institute for Wildlife Research, Department 162, 1412 Sixteenth Street, N.W., Washington, D.C. 20036-2266, or call (703) 790-4264.**