

EFFECT OF LONG DAYS ON MOLT AND AUTUMN MIGRATORY STATE OF SITE-FAITHFUL DARK-EYED JUNCOS HELD AT THEIR WINTER SITES

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Abstract.—Dark-eyed Juncos (*Junco hyemalis*) caught at their regular winter sites and then held outdoors fail to become restless or to fatten in the following autumn. Two alternative explanations for this failure to manifest the autumn physiological migratory state are (1) that the birds' perception of familiar characteristics of the migratory destination suppresses the autumnal state, or (2) that spring and summer daylengths in the winter range are too short to permit birds held there to complete the annual physiological cycle. We caught juncos in winter on their perennial winter home ranges, held them there during spring and summer, and then monitored their restlessness and fattening next autumn. We divided these winter-caught birds into three treatment groups. The first two were alike in being exposed indoors to long days simulating the photoregime of spring and summer on the breeding range. They differed in that we placed one of the two groups outdoors in view of the natural environment for ten days in late summer, just before monitoring began, whereas during those ten days the other group remained indoors and on the local photoregime until monitoring. The third group was held outdoors throughout spring and summer on the natural daylengths of their winter site. We compared these three site-faithful groups with each other and with juncos that we caught on the breeding range in late summer, displaced to the winter range, and monitored alongside the other groups. The summer-caught juncos fattened and became restless. The site-faithful group that remained indoors until monitoring exhibited a slight tendency to do so. The site-faithfuls that were placed outdoors after long days indoors and the site-faithfuls that spent spring-summer outdoors neither fattened nor became restless. Site-faithful groups exposed to artificially long days molted earlier than birds recently caught on the breeding range and also earlier than the site-faithfuls continuously held outdoors. Recently caught birds probably delayed molt because, although they had experienced long summer days, they had also reproduced. Our results indicate that the previously reported suppression of the autumnal migratory state in juncos held outdoors at the destination of the autumn migration is not attributable to the shorter daylengths the birds experience there during spring and summer. They are less helpful on the question of whether the suppression results from recognition of the winter site. Received 8 Dec. 1988, accepted 16 Nov. 1989.

Internal timing mechanisms are important for first-time migrants of some species. Such mechanisms apparently maintain the young bird in autumn migratory condition for a period sufficient to allow it to travel to the winter range of its species or population (e.g., Gwinner 1969, 1986; Berthold 1973, 1975; Berthold and Querner 1981; Ketterson and Nolan 1986). Much less is known of the regulation of subsequent migrations,

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including whether experience and learning replace or modify the timing mechanisms that control the migrations of naive individuals (Gwinner 1986; but see Stimmelmayer 1932, Sniegowski et al. 1988).

We repeatedly have found (Ketterson and Nolan 1983, 1987a, 1987b, 1988) that groups of site-faithful Dark-eyed Juncos (*Junco hyemalis*) caught in winter and detained until the following autumn outdoors on or near their perennial winter home ranges at Bloomington, Indiana (39°N, 86°W) failed to show the autumnal physiological evidence of readiness to migrate that is usual in captive birds. Throughout the fall they put on no migratory fat and exhibited little nocturnal restlessness (*Zugunruhe*). In the following spring, both fattening and restlessness were normal for that season, i.e., were at the levels exhibited by juncos not held over summer at their winter sites. In contrast, juncos caught in late summer on their Canadian breeding grounds, transported to Bloomington, and monitored there with the winter-caught site-faithful individuals both fattened and showed *Zugunruhe* in the autumn immediately after their capture (Ketterson and Nolan 1983, 1986). During the following autumn, after a year in captivity, these juncos again fattened and, to a lesser extent than the preceding year, became restless (Ketterson and Nolan 1987a). Finally, the suppression found in winter site-faithful juncos monitored in cages during autumn was also observed when site-faithful juncos were released at the beginning of autumn both at their migratory destinations and north of those destinations. Most of these birds remained where released, although a few returned to their winter home ranges (Ketterson and Nolan 1988). Interestingly, one individual that remained north of its usual winter site after release returned to its perennial site one year later. This, like the spring resumption of fattening and restlessness by birds that were suppressed in autumn, shows that the observed suppression of the migratory state was not permanent.

We attributed (Ketterson and Nolan 1983, 1986, 1987a) the differences between the site-faithful juncos and the Canada-caught juncos to site recognition. The former group had remained at the perennial destination of its autumn migrations—juncos that are site-faithful return at a rate strongly suggesting that all survivors return (Ketterson and Nolan 1983, 1986)—whereas the latter group almost certainly was not familiar with the region where we monitored them. In autumn, the site-faithful birds did not develop readiness to migrate, whereas the birds that were not on their winter home ranges did so (compare Sniegowski et al. 1988).

We recognized, however, another possible explanation for our results. Birds on artificial photoregimes that differ from those they experience in nature sometimes behave abnormally during the remainder of the annual

cycle (Wolfson 1960a, 1960b; Moore et al. 1982; Donham et al. 1983; Farner et al. 1983; Gwinner 1986). Juncos caught and held at their winter sites during the following spring and summer are exposed to shorter days than juncos on the breeding range. Thus, perhaps the site-faithfuls had not been exposed to days long enough to induce the migratory state. This possibility was not precluded by the fact that Canada-caught juncos had fattened and grown restless in autumn after a year's captivity in Bloomington (Ketterson and Nolan 1987a) because their breeding grounds (at 49°N) may have been south of the breeding grounds of the site-faithful juncos (unknown, but juncos breed well beyond 49°N, American Ornithologists' Union 1983). This possibility deserved a direct test. Accordingly, in the experiment reported here we performed photoperiodic manipulations to test the hypothesis that the summer daylengths of Indiana were too brief to elicit normal autumn physiology in site-faithful juncos caught in Indiana in winter but sufficed for juncos caught during summer in Canada at 49°N. Anticipating that longer days might induce fattening and *Zugunruhe*, we also varied the exposure of site-faithful juncos to local cues that might be associated with recognition.

METHODS

We divided subjects into four treatment groups based on differences in their histories in the period between winter 1983–1984 and late August 1984, when we began monitoring *Zugunruhe* and fattening. These differences are described below.

Group 1 (9 males), after capture in winter, was held until 28 March 1984 in large outdoor aviary cages (described in Ketterson and Nolan 1983, 1986). On that date, which is near the mid-point of the junco's spring migration at Bloomington (pers. obs.), the birds were placed together in a windowless compartment about 2 × 2 × 3 m in size. Two fluorescent lights on the ceiling produced 22 lux at 1 m above the floor. One light was turned on before the other to simulate morning civil twilight, and the opposite was done to simulate evening civil twilight (Nautical Almanac 1984). Between 28 March and 26 April the daily light:dark cycle of the room was changed gradually in an effort to subject the birds to the approximate daylengths they would have experienced had they been migrating northward from Bloomington toward latitude 52°N (Fig. 1). Thereafter, from 26 April to 10 August, the photoregime was that of 52°N (Fig. 1; longest day between civil twilights: 21 h 13 min). On 10 August, the birds were removed and taken, in the same building, to a room with windows; there they experienced natural Indiana daylengths. On 20 August, each was placed in a separate opaque bag and taken to its individual registration cage on the roof of the building (the setup and environment are described in Ketterson and Nolan 1983) and thereafter monitored.

Group 2 (9 males) was identical in its history to Group 1, except that on 10 August its members were taken from the artificially lighted compartment and returned to one of the original outdoor aviary cages until 20 August, when they also were put in individual cages on the roof. Thus for 10 days in mid-August these juncos were exposed to normal geophysical and celestial characteristics of the destination of their previous migration(s) and could view

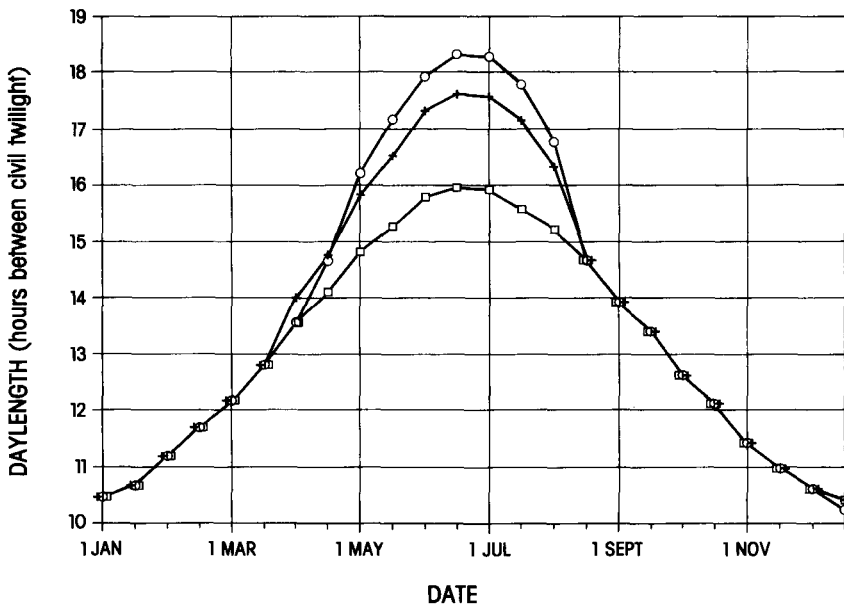


FIG. 1. Daylength according to treatment group. Lower curve depicts annual variation in daylength at Bloomington, Indiana and describes daylength experienced by Group 3 (see text). Upper curve refers to Groups 1 and 2 (see text) which were transferred indoors on 28 March and subjected to increasing daylengths to simulate a journey northward and then a breeding season at 52°N. On 10 August, Groups 1 and 2 were returned to natural Indiana daylengths. The middle curve refers to Group 4 (see text) and describes the daylengths that would be experienced by juncos that wintered near 39°N and then migrated during March to 49°N, the breeding latitude of the Group 4 juncos. Group 4 was transported southward to 39°N on 3 August.

the surroundings of the aviary. Reasons for this 10-day difference in treatment of Groups 1 and 2 will be given below.

Group 3 (9 males) juncos also were caught on winter home ranges near Bloomington where they had lived in at least one previous season and were placed in the large outdoor cages of the aviary. The aviary was 10–20 km from their winter home ranges and 1.5 km from the roof on which they were to be monitored in autumn. They were moved to individual outdoor registration cages on the roof on 20 August. Therefore these birds always experienced the natural Bloomington photoregime (longest day: 15 h 58 min, Fig. 1).

Group 4 (10 males) was caught in Wawa, Ontario (49°N), between 19 July and 1 August. In all probability the birds had bred at Wawa (longest day: 17 h 38 min, Fig. 1). On 2–3 August 1984 they were brought to Bloomington and held outdoors at the aviary until 26 August, when they were put in individual registration cages to be monitored. These Canada-caught birds differed from the winter site-faithful juncos in several ways that made them less than ideal controls, but we saw them as insurance: if they exhibited migratory physiology and all of the site-faithfuls did not, we could eliminate the possibility that some condition of our monitoring had suppressed restlessness and fattening.

The reason for exposing the Group 2 juncos to the outdoor environs of the aviary between 10 August and 20 August, while leaving the Group 1 juncos indoors, was as follows: Juncos housed indoors on long days may have been deprived of outdoor cues necessary to permit them to recognize that they were at their winter site, whereas juncos held outdoors on natural days were not deprived of such possible cues. This would introduce a confounding variable if it turned out that the experiment revealed differences between long-day and short-day juncos. The transfer of Group 2 to the aviary for 10 days was an attempt to expose these birds to outdoor cues and thereby eliminate or minimize the potentially confounding variable—difference in place of confinement—prior to the experiment.

Zugunruhe, molt, and fattening were measured as previously described (Ketterson and Nolan 1983, 1986, 1987a, 1987b). *Zugunruhe* was quantified for each individual by totalling with a microcomputer the number of 30-sec intervals of activity between the hours 21:00–04:30 (its nightly score). We then summed each bird's nightly scores over the full autumn (its seasonal total), counted the nights during which it exhibited activity for at least 30 minutes (its number of active nights), and noted the value of its nightly score on the night when it was most active (its maximum night). Monitoring of *Zugunruhe* began on 20 August (26 August for Group 4) and continued until 1 December, when an unauthorized person released all the birds and terminated the experiment somewhat sooner than we had planned (compare Ketterson and Nolan 1983, 1986, 1987a, 1987b).

Extent of fattening was determined in two ways. First, we computed for each individual the difference between its initial mass in late August and its maximum mass during autumn, as measured in a series of inspections about two weeks apart. This difference we express in absolute terms and also as a percentage of initial mass. Second, at each inspection we classified subjects according to amount of visible subcutaneous fat, employing a previously described scale of 0–5 (Nolan and Ketterson 1983). We have observed a high correlation between this index and fat extractable in the laboratory (Rogers et al., unpubl. data). Molt was monitored at each inspection, using methods previously described (Ketterson and Nolan 1987a).

We employed the Kruskal-Wallis nonparametric ANOVA to test for differences among groups. *A posteriori* multiple comparisons based on Kruskal-Wallis rank sums were performed as described in Sokal and Rohlf (1969). Because the multiple comparisons require equal sample sizes, we randomly eliminated (by assigning numbers and drawing lots) one male from Group 4 for these tests.

RESULTS

Zugunruhe.—In Kruskal-Wallis tests, groups differed in all measures of *Zugunruhe* (Table 1 footnotes). Group 4 was the most active and Group 1 the next most active, while Groups 2 and 3 exhibited almost no activity (Table 1, Fig. 2). In multiple comparisons of seasonal totals and numbers of active nights, Group 4 juncos were significantly more restless than Groups 1, 2 or 3 ($P < 0.05$) which did not differ from one another. For maximum nightly score, Group 4's score was greater than that of Groups 2 and 3 ($P < 0.05$) but not of Group 1 ($P > 0.05$). Group 1 also could not be distinguished from Groups 2 and 3 ($P > 0.05$) and hence was intermediate in maximum nightly score.

Body mass and fat class.—Intergroup differences in gain in mass (Table 2, Fig. 3) were significant (Kruskal-Wallis, $P < 0.05$). Multiple compar-

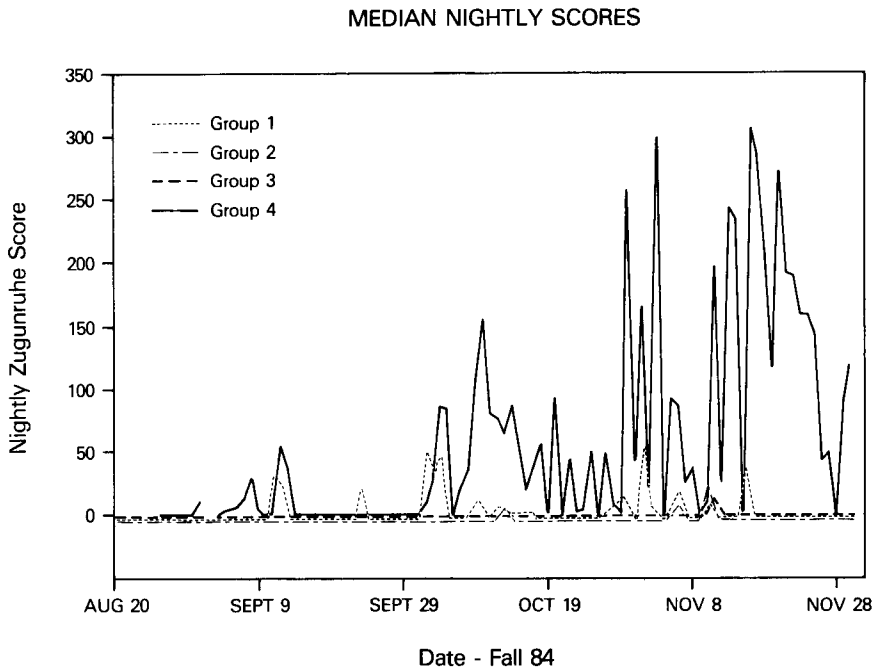


FIG. 2. Median nightly *Zuginruhe* scores according to date for Groups 1–4. The day-lengths experienced by the groups are described in the caption to Fig. 1. Groups differ additionally in that Group 1 remained indoors between 10 and 20 August and was thus given no exposure at this time to the environmental cues being experienced by Groups 2–4.

isons of absolute gain show that Group 4 made significantly greater absolute gains than Groups 1, 2, and 3, which did not differ from one another. In percentage gain (Table 2), Group 4 differed from Groups 2 and 3. Group 1 was intermediate; its gain could not be distinguished from those of Groups 2 and 3.

The median fat class (data not shown) of Groups 1–3 never exceeded 0.5 during the experiment, whereas the median fat class of Group 4 rose from 0.5 on 8 October to 3.0 on 8 November and was 3.5 at the end of the experiment.

Molt. — Although the date of first examination for molt was not identical for all groups, it is clear (Fig. 4) that Groups 1 and 2 began to molt earlier than Groups 3 and 4, probably about one month earlier. The conclusion that Group 4 birds molted later than Groups 1 and 2 is supported by further evidence: among 57 free-living adult juncos (including Group 4) that we caught and examined at Wawa during the period when we captured

TABLE 1
AUTUMN ZUGUNRUHE^a OF GROUPS^b OF DARK-EYED JUNCOS SUBJECTED TO PHOTOPERIODIC
AND OTHER TREATMENT DIFFERENCES IN 1984

	Seasonal total ^c median (extremes)	Maximum night ^d median (extremes)	Active nights ^e median (extremes)
Group 1	2154 (39–9015)	190 (17–687)	12 (0–31)
Group 2	204 (14–7578)	49 (5–431)	0 (0–30)
Group 3	308 (17–5332)	50.5 (3–320)	1.5 (0–29)
Group 4	6608 (2386–14,327)	500 (196–757)	27 (16–68)

^a Perch hops were monitored by microcomputer during 30-sec intervals between 21:00 and 04:30 (900 intervals per night) between 20 August and 1 December 1984. The sum of an individual's nightly scores is its seasonal score; its greatest nightly score is its maximum night; and nights in which its nightly score >60 are its active nights.

^b See Methods for descriptions of the groups.

^c Kruskal-Wallis, $H = 14.32$, $P < 0.003$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 1, 2, and 3 ($P < 0.05$).

^d Kruskal-Wallis, $H = 12.07$, $P < 0.001$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 2 and 3 ($P < 0.05$).

^e Kruskal-Wallis, $H = 12.87$, $P < 0.005$. Pairwise multiple comparisons non-significant except when Group 4 compared to Groups 1, 2, and 3 ($P < 0.05$).

Group 4, only one (possibly two) individuals had begun to molt in late July. By that date, all members of Groups 1 and 2 were well advanced in molt.

DISCUSSION

The most striking result of this experiment is the failure of any group of winter-caught site-faithful juncos (Groups 1–3) to become as restless or as fat as recently caught breeders from 49°N (Group 4), regardless of whether the site-faithful juncos had experienced the spring-summer photoregime of 39°N (Group 3) or of 52°N (Groups 1 and 2). These results indicate that exposure to the shorter summer days of the winter site cannot alone explain the suppression of autumn physiology in juncos held over summer at or near their winter sites. Thus, earlier reports of this suppression which were interpreted as possible evidence for recognition of the winter site do not need to be reinterpreted as simply an artifact of photoperiodic treatment. But the results of this experiment add little to answering the question of whether the suppression is properly attributable to recognition. We do not know when recognition, if that is what is responsible, takes place or what cues are required. If recognition can occur as late as late August or September and can take place from a small cage

ALL GROUPS BODY MASS

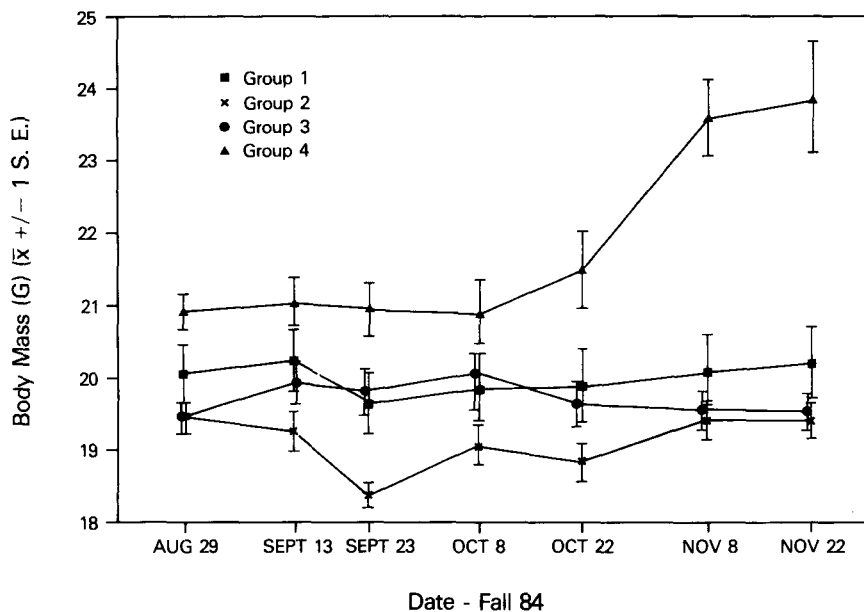


FIG. 3. Mean body mass ($\pm$ one SE) according to date for Groups 1-4 (see caption to Fig. 2).

TABLE 2
MAXIMUM GAIN^a IN BODY MASS, AUTUMN 1984, ACCORDING TO GROUP^b

	Absolute gain (g) ^c mean (extremes)	Gain as % of initial mass ^c mean (extremes)
Group 1	0.90 (-0.5-3.7)	5.0 (-2-19)
Group 2	0.20 (0-0.7)	1.0 (0-4)
Group 3	0.40 (-0.2-1.8)	2.0 (-1-10)
Group 4	2.5 (0.9-8.8)	12.0 (4-44)

^a For each individual, mass near the beginning of the experiment was subtracted from maximum mass attained thereafter. In a Kruskal-Wallis analysis of variance of absolute change, $H = 17.17$, $df = 3$, $P < 0.001$. In the same test of percentage change, $H = 16.37$, $df = 3$, $P < 0.001$.

^b See Methods for descriptions of the groups.

^c Multiple pairwise comparisons of groups were non-significant except when Group 4 was compared to Groups 1, 2, and 3 for absolute gain and to Groups 2 and 3 for percentage gain ($P < 0.05$).

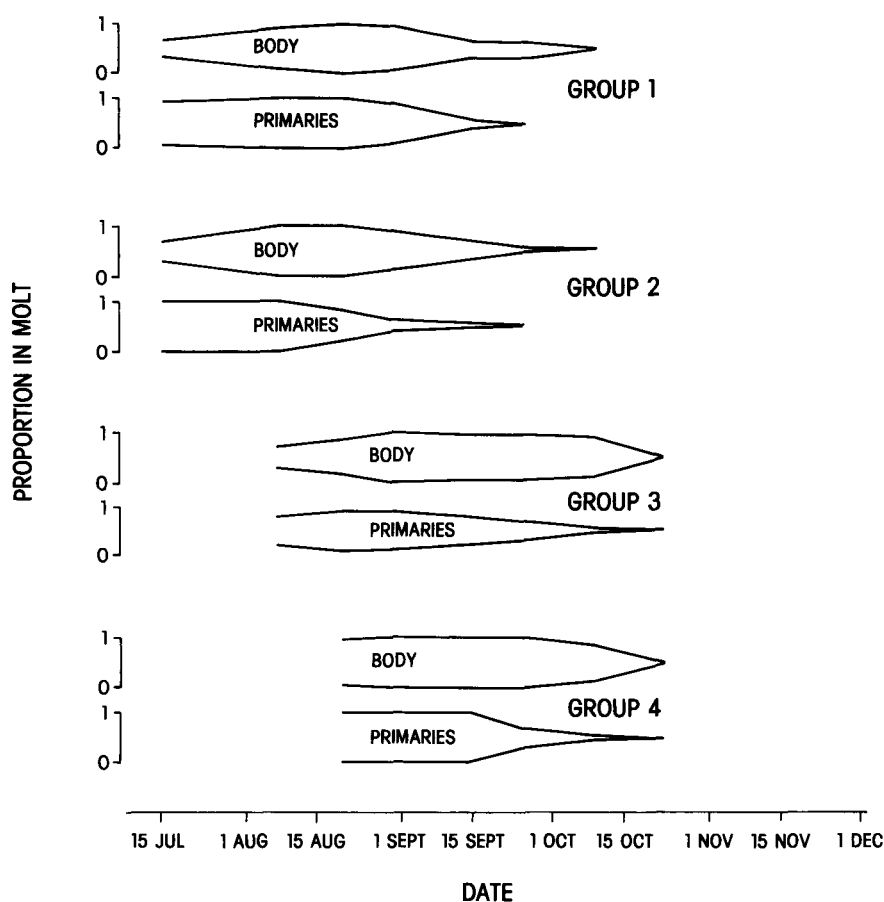


FIG. 4. Proportion in molt according to date for Groups 1–4 (see caption to Fig. 1).

on a roof, then the results of this experiment are consistent with recognition by Groups 1–3. If recognition requires cues not perceivable from the roof, and if we attach importance to the intermediate fattening and restlessness of Group 1, we might conclude that Groups 2 and 3 were suppressed by recognition, while Group 1, which went directly from indoors to a roof, was not fully suppressed. However, none of our experiments (Ketterson and Nolan 1987b, 1988) has provided any strong direct support for recognition.

In molt schedule, Groups 1 and 2 were alike and were much ahead of Groups 3 and 4, which were alike. Photoperiod has been shown to accelerate or retard molt, according to treatment (e.g., Moore et al. 1982),

yet Groups 3 and 4 were on different photoregimes. We doubt that the similarity of Groups 3 and 4 and their difference from Groups 1 and 2 were caused solely by the fact that Groups 1 and 2 spent most of the summer indoors, while Group 3 and 4 were outdoors. A more persuasive explanation of the timing of molt must take into account both the spring-summer photoregimes and the other summer experiences of all groups. Only Group 4 reproduced. Engaging in reproduction in Canada (Group 4) and experiencing short spring and summer days in Indiana (Group 3) apparently had about equal effects in delaying molt.

The fact that postnuptial molt was normal in its extent (i.e., complete), although somewhat differently timed in all site-faithful juncos, also confirms an earlier finding (Ketterson and Nolan 1987a). In the junco, the suppression of fattening and *Zugunruhe* can take place independently of molt. In contrast, in the White-crowned Sparrow (*Zonotrichia leucophrys*) molt is apparently a precondition for autumn fattening (Moore et al. 1982, Farner et al. 1983).

In sum, whatever suppresses normal autumn physiology in site-faithful juncos held at their migratory destination cannot be overridden solely by long summer days. If suppression has nothing to do with daylength but is caused by some other experience or by the absence of an experience, we suggest two experiences that our site-faithful juncos have lacked: none has made the migration northward in the spring preceding monitoring and none has had the opportunity to breed (but see Ketterson and Nolan 1987a).

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