Spring and summer confinement of dark-eyed juncos at autumn migratory destination suppresses normal autumn behaviour

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Abstract. A group of dark-eyed juncos, *Junco hyemalis*, caged during spring and summer on their wintering site of previous years, showed normal spring hyperphagia and fattening, migratory restlessness and post-nuptial moult, but the birds failed to fatten and become normally restless during the ensuing autumn migration season. A second group, treated similarly but not on their individual wintering sites, behaved as the first group except that they did become fat and restless at the appropriate time in autumn. It is probable that perception of the migratory destination suppressed normal autumn behaviour of the birds held at that destination. Experience may therefore play an important role in the regulation of the avian migratory state.

Study of the timing of bird migration has revealed the existence of two types of regulatory mechanism. In some species, seasonal information from the external environment drives the annual cycle. A period of short days prepares the bird for the start of a new year's cycle. The lengthening days of spring then trigger the cycle, which proceeds through moult (in many species), migratory readiness and gonadal growth; late summer and autumn events (gonadal regression, post-nuptial moult and autumnal migratory readiness) follow, completing the cycle without additional triggering, so far as is known. When held under constant photoperiodic conditions, such 'externally driven' species fail to cycle normally (review by Farner et al. 1983). Other species appear to depend upon an internal circannual clock, which causes phases of the annual cycle to begin and to end in appropriate sequence and at approximately the appropriate times, even when the external environment is held constant and thus supplies no information. Recent literature has emphasized this endogenously regulated group (e.g. Gwinner 1969, 1986; Berthold 1973; Berthold & Querner 1981; Biebach 1983) and, especially, the fact that hand-raised, inexperienced captives in a constant environment engage in migratory behaviour that corresponds in time of onset and duration with the migrations of free-living members of the same species or population.

Little attention has been devoted to the importance of experience in modifying either sort of regulatory mechanism, but at a certain stage of migration experience clearly plays some role. Birds commonly form attachments to particular sites and return to these in subsequent migrations, often reaching their destinations on different dates in different years depending on recent weather and other conditions (e.g. Nolan 1978). Arrival at the site occupied in the previous year causes migration to terminate, and experience thus accounts for annual differences in the timing of the end of the individual's migration behaviour. In this paper we ask whether experience can have a much greater effect. When a bird is treated so that its timing mechanism should dictate that it migrate but its previous experience should inform it that it is already at its destination, will the bird delete migration from its annual cycle altogether?

Ideal experimental design would use individuals whose breeding and wintering sites are both known. Subjects could then be caught at one seasonal site and transported just before a normal migration period to the other seasonal site; temporal information would then conflict with perception of the migratory destination. However, it is rarely possible to know both an individual bird's breeding home range and its winter home range. This is true of our experimental subject, the migratory dark-eyed junco, *Junco hyemalis*, whose breeding range is, essentially, most of Canada and whose winter range is most of the United States. In our experiments, therefore, in order to expose juncos to their winter home ranges just before they would normally migrate in autumn, we caught the birds in winter, held them on their winter sites until late in the following summer, then determined

whether they showed autumn migratory behaviour. As pointed out below, this long captivity at the terminal point of autumn migration raises potential problems in interpreting results.

We reported earlier (Ketterson & Nolan 1983a) that when four adult dark-eyed juncos were held during summer at their autumn migratory destinations (their winter home ranges) at Bloomington, Indiana, they subsequently failed to show the behaviour and physiology characteristic of captive migratory birds during autumn (Berthold 1975), i.e. they did not fatten or exhibit migratory restlessness (Zugunruhe). In contrast, a group of juncos that were caught on their Canadian breeding territories in late summer, brought to Bloomington, and monitored in the autumn alongside the birds held at their destination, did fatten and became intensely restless. Considering the great size of the junco's winter range (Ketterson & Nolan 1976, 1983b), it is very unlikely that the Canada-caught birds had previous experience in Bloomington. The following spring all individuals, wherever caught, became very restless and fat.

We suggested three possible explanations for the autumn differences between the two groups. (1) Because Indiana is south of the breeding range and the birds caught in winter (hereafter, Indiana juncos) were detained there for about 8 months before the experiment, they experienced unnaturally short spring and summer days, whereas the Canada-caught birds (Canada juncos) experienced the photoperiodic regime of a breeding latitude. Perhaps the Indiana juncos may have missed some photoperiodic stimulus necessary to induce autumn migratory physiology, such as days of a particular minimum length (Wolfson 1960a, b; Moore et al. 1982; Donham et al. 1983). (2) Confinement of the Indiana birds in groups during spring and summer had prevented them from engaging in both spring migration and reproduction. Perhaps they failed to experience some condition necessary to elicit migratory physiology in experienced migrants. (3) When the season for migration arrived, the Indiana birds were at the precise destination of earlier autumn migrations, whereas the Canada juncos were not. Perhaps the Indiana juncos' perception, prior to the migration season, of environmental features familiar to them as the end point of migration overrode or terminated prematurely the physiological state of readiness to migrate (but see Gwinner & Czeschlik 1978 for a result inconsistent with this suggestion). If so,

previous experience at the destination prevailed over the seasonal timing mechanism.

Two additional Canada-caught individuals were monitored in our earlier study (Ketterson & Nolan 1983a), but, unlike the other Canada juncos, both had been in captivity for as long as, and had been treated the same as, the Indiana juncos. Despite this, they fattened and grew restless, which supported explanation 3. However, sample sizes were so small that it seemed necessary to learn whether suppression could be induced again, and, if it could be, to know how a larger group of Canada birds would behave in autumn when they too were held captive at Bloomington over the preceding summer. We therefore caught a new group of site-faithful Indiana juncos, monitored their behaviour during the spring migratory season to discover whether it was normal, and monitored their behaviour again during the following autumn. We compared these birds with a subset of the same Canada juncos used in the first experiment. These birds had been in captivity longer than the Indiana birds, and neither group had bred preceding autumn monitoring. If under these conditions the Canada juncos again became fat and restless and the Indiana juncos again did not, the probable explanation of the suppression would be that presence at the migratory destination had overridden the timing mechanism responsible for autumn migratory condition.

BACKGROUND AND METHODS

Dark-eyed juncos of the eastern migratory race breed largely in Canada and winter throughout almost all of the eastern United States (Bent 1968; American Ornithologists' Union 1983). Autumn migration occurs between late August and about 1 December, spring migration between about 1 March and mid-May (Ketterson & Nolan 1982, 1985). Few individuals that are banded on their home range in one winter return there the following winter, but those that do continue to return as long as they live (Ketterson & Nolan 1982, 1985). This conclusion is based on the fact that the rate of return of such individuals in later winters is equal to the annual survivorship of juncos as determined by other, independent estimates (Ketterson & Nolan 1982, 1983b, 1985). It follows that once a junco has

been faithful to a winter site the destination of its future autumn migrations can be predicted with confidence.

During the winter of 1980–1981 we caught six ringed Indiana individuals, five males and one female, on or near the grounds of the Indiana University aviary and held them there in large outdoor cages until late February 1981. All had spent the preceding winter, 1979–1980, living free at this same location, thus demonstrating fidelity to the site. A second group (four males and six females) consisted of nine (spring 1981) or 10 (autumn 1981) Canada birds, which were a subset of the birds used in our earlier experiment (Ketterson & Nolan 1983a). These birds had been in captivity since July 1980, held either in individual registration cages (autumn 1980) or in the same outdoor aviaries as the Indiana birds (winter 1980–1981). Their breeding sites were near Wawa, Ontario, Canada (49°N, 85°W), but their previous individual wintering sites were unknown. The breeding sites of the Indiana birds were unknown.

We first compared the birds in spring, a few weeks after the Indiana group was captured. On 26 February 1981, all of the birds were moved to individual cages for registration of Zugunruhe (they could hear but not see one another) and left there until 8 June, when we returned them to the large aviary cages in which they lived together. The cages have been described previously, as have the locations, magnetic fields, views of the sky and views of other landmarks from the two kinds of cages (Ketterson & Nolan 1983a).

The next comparison began on 21 August 1981. Our object here was twofold: to compare the Indiana with the Canada juncos and to compare the Canada juncos in 1981 with themselves in 1980. All of the birds were again placed in individual cages, and their Zugunruhe was monitored from 25 August 1981 until 5 January 1982.

Zugunruhe was monitored and scored as before, except that in autumn 1981 we employed an Apple II microcomputer rather than Esterline-Angus event recorders. Our measure of Zugunruhe was the number of 30-s intervals per night during which an individual hopped on or off its perch at least once between 2100 and 0430 hours (hereafter, its nightly score; the maximum possible was 900). For each individual we noted its maximum nightly score, the sum of its nightly scores during the experiment (its seasonal score), and the number of

nights it activated its perch during at least 60 of the 30-s intervals (its number of active nights).

For our 1980 experiment we presented Zugunruhe data from only 2 nights per week, separated from each other by 2, 3, 2, etc. nights (Ketterson & Nolan 1983a). For spring 1981 we did the same ($N = 30$ nights), but in autumn 1981, with one exception, we scored all but the few nights in which there were mechanical failures ($N = 113$ nights). The exception is that when we compared the autumnal Zugunruhe of the Canada individuals that were experimental subjects in both 1980 and 1981, we matched the behaviour of each individual in the two autumns and accordingly used values for only 2 nights per week ($N = 32$ nights, the same dates in each year).

Analysis of Zugunruhe of male and female juncos has revealed only slight sexual differences (Ketterson & Nolan 1985). In the experiments reported here, these were non-significant, and we have therefore pooled data without regard to sex. Juncos in their first autumn of life may be less restless than older juncos (Ketterson & Nolan 1985); all experimental subjects were in at least their third autumn of life in 1981.

Birds were weighed when they first entered the experimental cages and approximately bi-weekly thereafter, always in mid-afternoon. Visible subcutaneous fat deposits in the furcula and on the abdomen were scored from 0 to 5, as previously described (Nolan & Ketterson 1983). To compare changes in body mass between groups, the average difference between initial mass and maximum mass was computed for each group, limiting the autumn analysis to mass attained by 1 December, after which migratory fattening and winter fattening cannot be distinguished. To compare the Canada birds in 1981 with themselves in 1980, we used a different method. These individuals had been unusually lean at the start of the 1980 experiment, presumably the result of the stress of having recently been transported to Indiana. We therefore compared their fattening in 1980 and 1981 by matching each individual's body mass and fat class towards the end of the two autumns (1 December 1980 and 27 November 1981).

Each time a bird was weighed in autumn, its moult was examined until post-nuptial moult was completed. The most useful bases for comparison were moult of the primaries, which can be quantified, and of the ventral tract, which is typically the

Table I. Spring Zugunruhe scores, 1981

	Median* (extremes)		
Group	Seasonal total	Maximum night	Nights ≥60
Indiana juncos (N=6)	6557 (2819–12 131)	571 (341–893)	20 (10–21)
Canada juncos (N=9)	9113 (1705–11 926)	766 (230–837)	20 (9–24)

* No significant difference between Indiana and Canada juncos on any measure.

last tract renewed. Each primary was given a value of 0 through 5, as follows: 0 = not yet moulted; 1 = missing, no renewal; 2 = short quill appearing; 3 = 20–50% of final (full) length; 4 = at least 60% of full length, but not complete; 5 = complete. Values of the nine primaries of the individual's right wing on any particular date were summed, so possible scores ranged from 0 to 45. For the ventral tract we recorded whether sheaths were present on at least four or five feathers, and, if so, we classified moult as incomplete.

Most statistical comparisons were by rank-order statistics, with the lowest score ranked 1. In one exception, we used Fisher's exact probability test to compare the timing of post-nuptial moult. In the other exception, comparison of body mass of Canadian individuals in successive autumns was by a *t*-test of differences between matched pairs. In all tests the criterion for significance was $P < 0.05$, two-tailed.

RESULTS

Indiana Versus Canada Juncos, Spring 1981

The Zugunruhe of the two groups of juncos in spring 1981 was indistinguishable (Mann–Whitney *U*-test) for seasonal score, maximum nightly score and number of active nights (Table I). Figure 1 shows the median nightly score per group throughout the spring. Canada juncos became restless somewhat earlier in the season, but in other respects the Indiana birds resembled the Canada juncos and were normally and intensely active at night.

All of the birds were lean when placed in the registration cages, as is normal for juncos held captive in large groups in late winter; all appeared
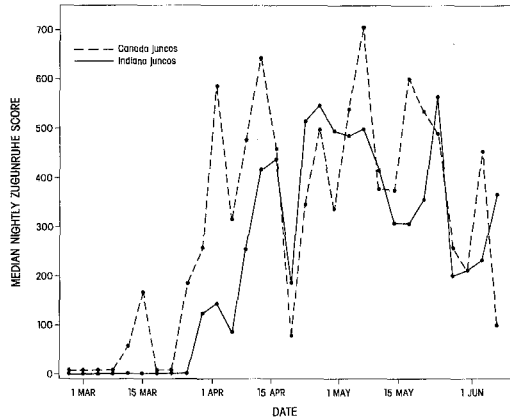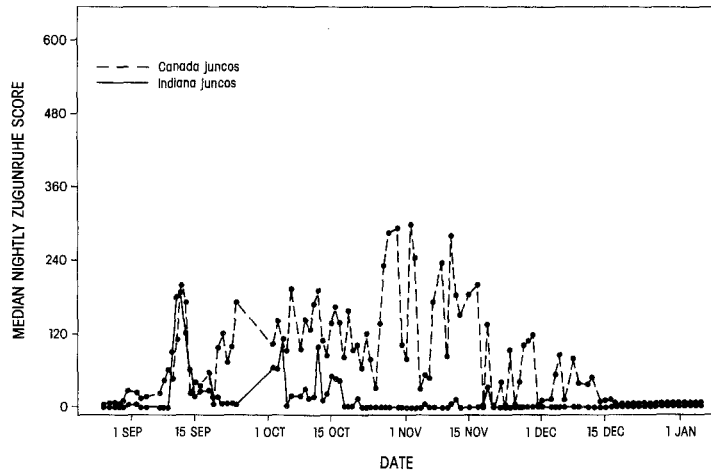

Figure 1. Median nightly Zugunruhe score of six Indiana juncos and nine Canada juncos, according to date, spring 1981. Indiana juncos were caught during winter 1980–1981 and held on the winter home range. Canada juncos were caught on their breeding ground in July 1980 and transported to Indiana, where they were held with the Indiana juncos. For other details see text.

Table II. Autumn Zugunruhe scores, 1981

	Median (extremes)		
Group	Seasonal total*	Maximum night	Nights ≥60*
Indiana juncos (N=6)	2439 (259–10 377)	313 (112–503)	12 (2–39)
Canada juncos (N=10)	10984 (2549–31 728)	494 (165–853)	50 (19–76)

* In Wilcoxon summed ranks tests, groups differed in seasonal total ($P = 0.02$) and nights ≥ 60 ($P = 0.002$).

healthy. Members of both groups fattened greatly during the migratory season, and the Indiana juncos became the fatter of the two: their mean gain in mass was 5·6 g (a mean 29·7% increase over their mass at the start of the experiment), as opposed to a mean 4·0-g gain by the Canada juncos (mean 20·8% increase; Mann–Whitney *U*-tests, $P < 0.05$ for difference in percentage change; difference in absolute change NS). At their fattest, the Indiana birds had visible deposits of almost 4 (median), the Canada birds of slightly over 3.

Figure 2. Median nightly Zugunruhe scores of six Indiana juncos and 10 Canada juncos according to date, autumn 1981 (see legend to Fig. 1). For other details see text.

Table III. Change in body mass, 20 August–27 November 1981

Group	Mean (extremes)	
	Absolute gain (g)*	Gain as a % of initial weight*
Indiana juncos (N=6)	0 (−1·2–1·5)	0 (−6–8)
Canada juncos (N=10)	3·9 (2·0–6·4)	19 (10–28)

* In Wilcoxon summed ranks tests, groups differed in absolute gain and relative gain (P<0·001).

Indiana Versus Canada Juncos, Autumn 1981

Canada juncos became consistently more restless and fatter than Indiana juncos in the autumn (Wilcoxon summed ranks). Table II presents the median and extremes of nightly scores, seasonal scores, and number of active nights. Figure 2 shows the median nightly Zugunruhe scores of groups throughout the season: Canadian birds were conspicuously more restless. Activity of Indiana juncos was largely concentrated in early September while the birds were still in moult, a pattern that we also observed in autumn 1980 (Ketterson & Nolan 1983a).

Table III shows the average maximum gain in mass, and Fig. 3 the seasonal progression of change in body mass, of the two groups. Again the groups differed. The maximum visible fat class also differed (Fig. 4). From class 0 (the class of all 16 birds at the beginning of the experiment), half the Indiana group reached a maximum class of 1 and the other half reached a maximum class of 2. Six of the Canada group attained a maximum class of 3, and the remaining four reached class 5.

Group differences in fattening were not restricted simply to the amplitude of change; the time course also differed. The Canada birds fattened gradually and increasingly throughout the autumn and were heaviest in late November, while the body mass of the Indiana group peaked nearly a month earlier, then varied erratically until winter fattening began in December (Fig. 3). In the Canada group there was no connection between attainment of maximum body mass and the date when nightly score of Zugunruhe was highest (compare Figs 2 and 3), but what peaks of fattening and restlessness the Indiana birds did show occurred on about the same date, in mid-September (Figs 2 and 3).

All of the birds were well along in moult on 20 August, but none had completed primary moult ($\bar{X}$ moult score of Canadians $\pm$ SD $= 39\cdot6 \pm 3\cdot57$; $\bar{X}$ moult score of Indiana site-faithfuls $\pm$ SD $= 32\cdot1 \pm 3\cdot39$). Indiana birds tended to be less advanced, but not significantly so (Mann–Whitney $U = 16\cdot5$, NS). This tendency persisted throughout moult; only two of the Canada juncos still exhibited
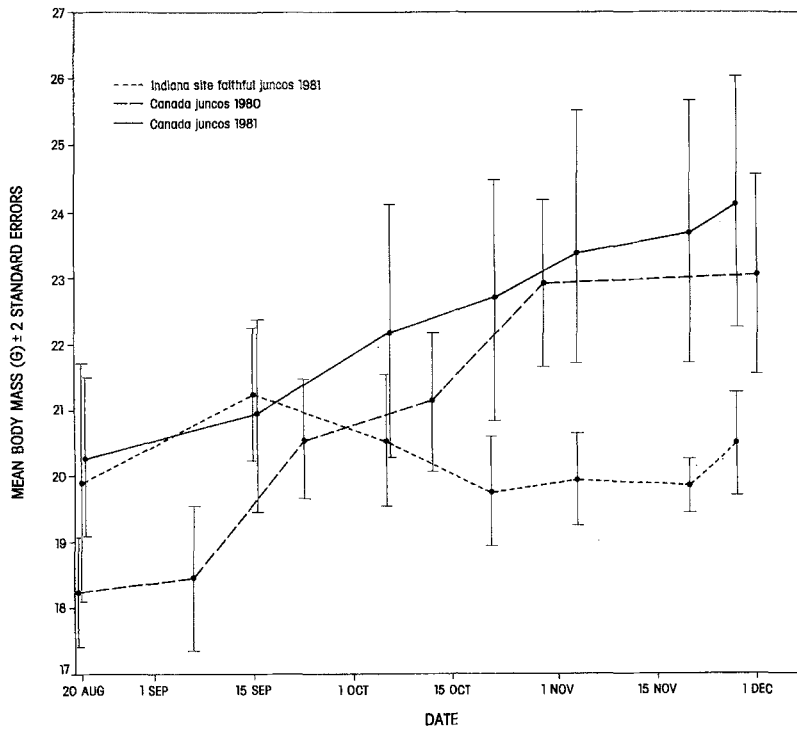
Figure 3. Mean body mass (± 2 SE), according to date, of 10 Canada juncos (see legend to Fig. 1) in 1980 and again in 1981, and of six Indiana juncos (see legend to Fig. 1) in 1981.
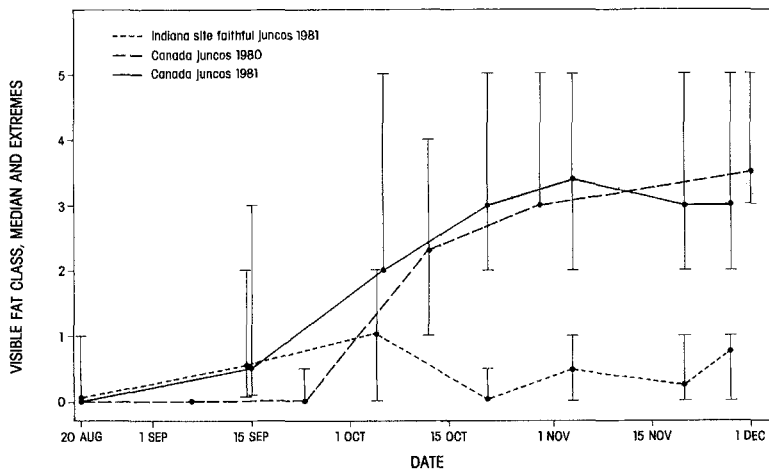

Figure 4. Median fat class (and extremes), according to date, of 10 Canada juncos (see legend to Fig. 1) in 1980 and again in 1981, and of six Indiana juncos (see legend to Fig. 1) in 1981.

Table IV. Autumn Zugunruhe scores of 10 Canada juncos measured both in 1980 and 1981

	Median (extremes)		
Year	Seasonal total*	Maximum night*	Nights ≥ 60*
1980	6517 (1023–12 933)	641·5 (247–828)	21·5 (6–28)
1981	3385 (749–9018)	370·5 (165–814)	16 (5–23)

* In Wilcoxon matched-pairs signed-ranks tests, years differed in seasonal total ($P < 0.01$), maximum night ($P < 0.05$), and nights ≥ 60 ($P < 0.01$).
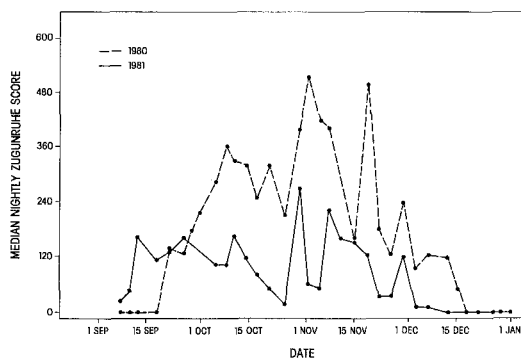
Figure 5. Median nightly Zugunruhe scores, according to date, of 10 Canadian juncos (see legend to Fig. 1) in autumn 1980 and again in autumn 1981.

traces of ventral moult on 5 October, whereas four Indiana birds did so (Fisher's exact, $P = 0.08$). One was still moulting on 21 October.

Canada Juncos, Autumn 1980 Versus Autumn 1981

Scores of Zugunruhe of Canada juncos were significantly lower (Wilcoxon matched-pairs signed-ranks test) in their second autumn in captivity than in their first (Table IV, Fig. 5). Restlessness began and ended about 2 weeks earlier in 1981 than in 1980. The earlier start may have been associated with a slightly earlier moult in 1981 than in 1980 (see below); we cannot explain the earlier finish, but note that similarly treated birds behaved similarly in 1980 (Ketterson & Nolan 1983a, group 2).

Changes in body mass followed about the same time course in the 2 years, but were somewhat greater in 1981 (Fig. 3). Although the median fat class was 4 in 1980 and 3 in 1981, mean maximum body mass was 23·55 g in 1980 and 24·35 g in 1981. These differences were not significant (Wilcoxon matched-pairs signed-ranks test).

Moult appeared normal in both years, with a tendency for some individuals to complete moult slightly earlier in 1981 than in 1980. These birds had bred in 1980, which probably delayed the onset of moult in that year (Newton 1966; Nolan 1978).

DISCUSSION

Indiana site-faithful juncos detained over summer at the destination of their autumn migration failed to show typical autumnal indications of readiness to migrate. The Zugunruhe and fattening of these birds had been monitored in the previous spring and were normal for that season. In contrast, Canada-caught juncos that almost certainly had no previous winter experience at the Indiana site where they were detained exhibited greater autumnal readiness to migrate than did the site-faithful birds. The Canada juncos, like the Indiana juncos, were in at least their third autumn of life and had been in captivity even longer than the Indiana juncos. None of the birds had lived in a group during the first 6 or 7 weeks of the breeding season (i.e. May and half of June); they were isolated in registration cages. Thus, the suppressed state of the Indiana site-faithful birds cannot readily be attributed to advanced age, to any effects of prolonged captivity, or to group-living during spring.

What is the likelihood that Indiana's short spring/summer days account for the result? Prolonged exposure to shorter-than-normal days has suppressed or arrested autumnal progression through the annual cycle in juncos (Wolfson 1960a, b) and other bird species, most notably the white-crowned sparrow (*Zonotrichia leucophrys gambelii*; Moore et al. 1982; Donham et al. 1983; Farner et al. 1983; compare Gwinner 1986 for a suppressive effect of longer-than-normal winter days on spring migratory physiology of pied flycatchers, *Ficedula hypoleuca*). Although the Canada and the Indiana juncos experienced the same photoregime from about 1 December onward and nevertheless differed in autumn fattening and restlessness, it is possible that the photoperiodic requirements of the

two groups were not the same. The Canada juncos bred at latitude 49°N, which is also likely to have been the approximate latitude of their natal sites. If the Indiana birds derived from a population that bred substantially north of 49°N, they may have required longer spring and summer days than the Canada juncos to enter the migratory state.

Pending a direct test, we think this supposition unlikely because both Canada and Indiana juncos passed through the post-nuptial moult. Farner et al. (1983) stressed that for *Zonotrichia* the complex of late-summer functions (onset of photorefractoriness, post-nuptial moult, pre-migratory fattening and migratory behaviour), when under photoperiodic manipulation, is tightly coupled and is expressed only in an all-or-nothing fashion. A lighting regime that induces one function induces all the others, and the same is true of suppression. Our report of moult without fattening may, therefore, represent the first uncoupling of these functions, and it suggests that Indiana daylengths were sufficient to induce the entire complex. It would follow that the suppression of Zugunruhe, hyperphagia and fattening was the result of some other environmental factor.

The reduced Zugunruhe of the Canada juncos in 1981 might indicate that their long captivity in Bloomington had caused them to form some attachment to that location comparable to the one proposed as responsible for the suppression in the Indiana birds. However, the fact that the Canada juncos fattened normally in 1981 speaks against this possibility, and we can only suggest that long captivity in itself may reduce restlessness. A comparable reduction has been reported for juncos by Swanson (unpublished data).

If we are correct that suppression in the Indiana juncos was based on recognition, then certain predictions follow: birds whose destination is known to be other than Indiana should not exhibit suppression when held in Indiana, and Indiana birds should not show it when held elsewhere. We are currently testing these predictions. We are curious, of course, as to how the juncos might have recognized their destination, but are reluctant to speculate because we do not know when the postulated recognition took place and because the sensory information available to the birds varied seasonally. In late spring the birds were on the roof of a building (Ketterson & Nolan 1983a). If they perceived at that time that they had not left their winter quarters and this was the basis of the later

suppression, then the perception may have relied on celestial or olfactory cues (the magnetic field on the roof is distorted and the visible landmarks unfamiliar; Ketterson & Nolan 1983a). In late summer, on the other hand, the birds were outdoors on their winter home ranges. If they perceived then that they had 'arrived early' on their winter sites, they might have made use of a variety of familiar cues. By early autumn they were again on the roof and again had access to only limited information.

Whatever the cues and whenever they had their effect, how might they have influenced the physiological expression of readiness to migrate? If we assume a neuroendocrine basis to migration (see Meier & Ferrell 1978 for a review) that is analogous to that for incubation, then expression of the behaviour would depend upon some combination of timed internal state, perception of external stimuli and the modifying influence of experience (e.g. Silver 1980, 1983; Michel & Moore 1986). In juncos there is weak evidence for a timed internal state: duration of restlessness in captivity corresponds to the season for migration, and sex- and age-related differences in duration tend to correspond to differences in the distance migrated by sex–age classes in nature (Ketterson & Nolan 1985). External stimuli also influence expression of restlessness in captive juncos: inclement weather is apparently suppressive (Ketterson & Nolan 1985); food shortage and subordinate social status are apparently stimulatory (Terrill 1987). In nature, migration is also likely to be influenced by food supply, density and characteristics of conspecifics, time of onset of winter weather and the like. It is among birds motivated to return to the destination of a previous year that experience must come into play. Upon reaching that destination, perception and recollection of characteristics learned during earlier residence presumably inhibit whatever neuroendocrine mechanism has been sustaining the migratory state. In the case of the suppressed juncos in this study, which never became fat or restless, the mechanism for termination may have been triggered prior to or simultaneously with the mechanism for initiation.

This speculation and our results partly agree and partly disagree with Terrill's model (1987). Terrill proposes that the junco's autumn migration is based, first, on an obligatory phase which causes the individual to travel some minimum distance into the northern part of the winter range. A

second, facultative phase responds to environmental conditions encountered after reaching the winter range and determines how far southward the bird settles in a particular year. Our data appear to emphasize the facultative nature of the migratory state and to challenge the notion of an inevitable or invariable first-phase migration. If recognition of the destination can override the migratory state altogether, learning and memory are more important in regulating migration than has previously been thought.

ACKNOWLEDGMENTS

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