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Experiments on Winter-site Attachment in Young Dark-eyed Juncos

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Abstract

Site attachment in young birds has sometimes been considered to take place during a sensitive phase as the result of an imprinting-like process. We conducted two four-year-long experiments on winter-site attachment in young migratory dark-eyed juncos (*Junco hyemalis*). In both, we caught birds over a range of dates, displaced them to large outdoor enclosures, and released them near the end of winter. In the first experiment, release was at the capture site and all returns next winter were to that site. The return rate did not vary with date of capture and confinement; therefore attachment could have been completed either before capture or after release. The absence of returns to the confinement site suggests that attachment to a place requires that the individual live free there. In the second experiment, release was at the confinement site, and many subjects remained there, probably until they migrated northward. Returns next winter were to both the capture site (the majority) and the confinement-release site. The fact that a few juncos formed a bond to the confinement-release site in this experiment reinforces the view that living free is necessary for site attachment. Individuals caught and confined earlier in winter tended to be less likely to return than those caught later. The distribution of returns according to date of capture indicates that attachment was completed at different dates in different subjects, which is not consistent with imprinting during a clearly defined sensitive period. However, young juncos hatch and migrate at various dates. Therefore our experiment does not rule out the existence of a brief sensitive phase for site attachment, its dates varying among individuals because age and/or timing of migration vary.

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Introduction

Probably because studies conducted in the reproductive season far outnumber those in the nonbreeding season, it has only recently become apparent that year-to-year fidelity to the winter home range is widespread across avian taxa (KING 1969; RAPPOLE et al. 1983; METCALFE & FURNESS 1985; CHRISTMAS et al. 1986) and may be as common as breeding-site fidelity. Similarly, while attention

has been given to the formation in late summer of the migrant's attachment to the vicinity of its prospective breeding site, only one set of experiments (RALPH & MEWALDT 1975) has studied formation of the bond that causes the migrant to return in later years to its first wintering site.

In this paper we report two experiments investigating winter-site attachment in young (hatched during the preceding breeding season) migratory dark-eyed juncos (*Junco hyemalis*). In the first, we displaced individuals at various dates, confined them in outdoor cages where they could see free-living conspecifics, and in late winter returned them to and released them at their original capture sites. No attachment developed to the displacement-confinement site; all returns next year were to the capture-release site. We next held new groups of juncos at the same displacement-confinement site as before and liberated them there in late winter instead of releasing them at the capture site. Among those that returned next autumn and winter, a few did so to the confinement-release location, but most returns were to the capture site. From the relationship among rate and place of return, date of capture, and duration of confinement, we attempt to infer whether the underlying learning process was rapid and took place during a brief developmental sensitive phase or was gradual and variable among individuals.

Experiment 1

In a classic set of experiments, LÖHRL (1959, 1962) confined recently fledged collared flycatchers (*Ficedula collaris*) in outdoor cages and released them at different ages and in different places. None returned next year to the site of confinement unless they had been released there prior to the age at which autumn migration normally begins. Further, some young that LÖHRL displaced to unfamiliar locations and released there just before autumn migration returned next year to the release sites. LÖHRL concluded that attachment to the vicinity of the future breeding site occurs as the result of a process of imprinting and that it takes place only if the subject lives free at the site before migrating. (Compare the similar results and conclusions of BERNDT & WINKEL 1980, and SOKOLOV 1976, 1982, 1984, 1986, 1988 based, respectively, on experiments with young pied flycatchers, *Ficedula hypoleuca*, and chaffinches, *Fringilla coelebs*). No previous experiment has investigated the effect of confinement on formation of a bond to the winter site, which was the object of this experiment.

Methods

Distribution, Migration, and Winter-site Fidelity of Juncos

Migratory dark-eyed juncos in eastern North America breed largely in Canada and winter in southern Ontario and most of the eastern United States (BENT 1968). Bloomington, IN (39°N), the location of our study, lies slightly north of the latitudinal mid-line of the winter range (KETTERSON & NOLAN 1983a, 1985). Winter residents usually begin to arrive there in mid-Oct., and normal autumn migration ends about 1 Dec. (KETTERSON & NOLAN 1976). Spring migration begins about 1 Mar., but banded winter residents often remain at Bloomington into Apr. (KETTERSON & NOLAN 1983a: Table 3).

Our banding operations since 1957 indicate that juncos typically remain near their initial late-autumn capture site throughout the entire winter (but see the views of TERRILL 1987). However, fidelity to the same site in successive winters is much less widespread: annual survivorship is about 50 % (KETTERSON & NOLAN 1982, 1985), which greatly exceeds the return rate to the previous winter site. For example, in the early winters of 1981—82 through 1984—85 we caught, banded, and immediately released 499 young male juncos (unpubl. data). In month-long, intensive capture efforts in the following winters we recaptured 28 (5.6 %) of these nonexperimental birds (see also percentages in KETTERSON & NOLAN 1982). Observational evidence (KETTERSON & NOLAN 1982) and experimental results (NOLAN & KETTERSON in prep.) indicate that low site fidelity, not high mortality of young, is responsible for the low rate of return.

Capture, Confinement, Release

Between 10 Dec. and 10 Jan. 1981—82 through 1984—85, we caught and banded young juncos at several baited sites within 13 km of the Indiana University aviary. We sexed and aged these by methods previously described (KETTERSON & NOLAN 1976, 1982), and, except in 1981—82, included both males and females in our samples. The sex ratio did not vary with date, and the return rate next year did not vary with sex. Therefore data for the sexes were pooled (total 477 cases).

Captives were housed in large outdoor flight cages at the Indiana University aviary (described in KETTERSON & NOLAN 1983 b). The aviary grounds, which are occupied in winter by many free-living juncos, are visible from all cages. Each cage held 25—30 birds and was freely provided with food, water, vitamins, grit, and shelter (cut conifers). Juncos are gregarious in winter, and our subjects quickly adjusted to captivity.

During two or three days between 1—19 Mar., we let each bird go at its capture site, where we provided abundant food (cracked corn). The annual variation in date of release was caused by variation in weather. No releases were made when snow was predicted or was on the ground, or during precipitation. Just before release, we inspected all birds and withdrew from the experiment a few whose body mass was low.

Recapture

Recapture efforts were made each winter after 1981—82, both at the aviary and at all capture sites. On the aviary grounds we trapped and netted regularly throughout all the winters. At the capture sites, during two of the years (1982—83 and 1983—84) we caught birds only until 10 Jan.; in the other two years efforts continued throughout winter.

Results

Pooling across years, 21 of the 497 subjects (4.4 %) returned and were recaptured, all of them at their capture-release sites. We made 3013 captures of juncos (counting an individual once each time we caught it) at the displacement-confinement site, but we caught no subject there.

Variation in the date the individual was captured and confined was not associated with the probability of return the following year. 13 of 246 juncos caught 10—20 Dec. returned (5 %), 3 of 95 caught 21—30 Dec. returned (3 %), and 5 of 136 caught 31 Dec.—10 Jan. returned (4 %).

Discussion

The failure of young juncos to become attached to the site where they were confined, although it was located in suitable habitat occupied by conspecifics, is consistent with the results of LÖHRL (1959), BERNDT & WINKEL (1980), and SOKOLOV (1976, 1984, 1982, 1986). As reported below, in Exp. 2 some displaced birds that we released at the site of confinement did return there next year, and we

conclude that living free is necessary for formation of a winter-site bond in young juncos.

We are aware of no discussion of the reason why young migrants do not develop a bond to a site if their only experience there is in confinement. Clearly, caging is not so aversive that it causes the area to be avoided. Juncos that have been liberated after weeks of confinement often re-enter their cages when the doors are left open. (See also the results of Exp. 2.) If LÖHRL was correct that site attachment is the product of imprinting, the requirement that the individual move about the site may be analogous to the requirement that young nidifugous birds follow the object on which they are to become imprinted (e.g., HINDE 1970).

A more general explanation is suggested by studies of self-produced locomotion and related work. These have demonstrated that movement as the result of the subject's own efforts is either necessary to or important for the ability to encode (or use) spatial information. Thus, young animals moved passively through an environment (e.g., kittens on carousels in HELD & HAIN's 1963 classic experiment) fail in spatial tasks that can be performed by controls that have propelled themselves along the same paths (for humans see KERMOIAN & CAMPOS 1988; FOREMAN et al. 1983, 1990; CAMPOS & BETENTHAL, in press). Similarly, active exploration of a feeding apparatus is necessary to enable young adult rats (*Rattus norvegicus*) to find food in the apparatus (ELLEN 1987; STAHL et al. 1987; FOREMAN et al. 1990; for more general treatment of the development of cognitive maps see BAKER 1978; WILTSCHKO & WILTSCHKO 1978, 1987). Black-capped chickadees (*Parus atricapillus*) that watch another individual cache food are no more efficient than nonobservers in subsequent efforts to discover the cache (BAKER et al. 1988). "Perceptual and motor experience involved in the act of traveling to a cache location may be necessary for the establishment of spatial memory" (BAKER et al. 1988).

The second interesting result of Exp. 1 is that probability of return showed no correlation with date of capture and confinement. Assuming that the average date of terminating migration was about the same for birds caught 10–20 Dec. and those caught later, early-caught juncos had less experience on their winter home ranges before being confined. Yet this did not affect their rate of site fidelity. This could mean a) that experience prior to 10 Dec. was the basis for site attachment, or b) that the attachment formed after release in late winter, or c) that the process was completed before capture in some individuals and after release in others. Exp. 2 discriminates among these possibilities.

Experiment 2

The only previous experimental study of the site to which passerine birds return after being displaced and released in the preceding winter appears to be the work of RALPH & MEWALDT (1975). These authors caught two species of crowned sparrows (*Zonotrichia*) at various dates and displaced and released them immediately. Among young, the rate of return to the capture site next year was lower for individuals displaced in early winter, and some early-transported young returned

next year to the displacement-release site. As RALPH & MEWALDT noted, natural mortality may have been greater among early-released birds, because the interval between their release and autumn migration next year was longer than the interval between late release and migration. Nevertheless, it also seemed probable that a site bond had not yet had time to form in many sparrows displaced in early winter. RALPH & MEWALDT (1975: 704) concluded that attachment had many characteristics of imprinting and was, "at the very least, a rather special form of learning."

Because we released all our subjects simultaneously late in winter (a staged-delayed-release, KETTERSON & NOLAN 1990), our experiment avoids two possibly confounding elements in RALPH & MEWALDT's design. 1) The duration of exposure to mortality between release and possible return next winter was the same for all our birds. 2) The likelihood was reduced (see Results) that subjects might home to the capture site immediately after release (compare RALPH & MEWALDT 1976; BENVENUTI & IOALÉ 1980; see SCHWARTZ 1963) and gain experience there that could increase site fidelity the following winter.

Methods

Methods were the same as in the previous experiment except as here described. In the winters 1983—84 through 1986—87, we caught young juncos of both sexes at five baited locations between 5.2 km and 12.8 km from the aviary. Annual numbers of experimental birds, in chronological order, were 148, 120, 172, and 168 (total 608).

Catching and holding began on 1 Dec. and ended on 31 Jan. To distribute the sample as evenly as possible over this period (see Table 1), we divided it into six intervals (10 or 11 days long) and in each interval intensified or slackened our capture efforts as our success varied. We caught birds at all five sites in each interval to minimize possible bias arising out of qualitative differences among sites.

In the period 16—23 Feb. (depending each year on the weather) we opened the cages and let the birds escape to the aviary grounds, where we distributed abundant food. To learn whether they then homed to the capture site after release and before migrating, in all years but 1983—84 we trapped and netted at all capture sites and at the aviary. To detect individuals that returned next winter (1984—85 through 1987—88), we captured birds two or three times weekly at all these same sites from Nov. through Mar.

We distributed cases of return to the capture site among the six 10- or 11-day intervals described above and tested for a relationship between interval of capture and return the following year, using SAS logit analysis (SAS INSTITUTE INC. 1985). This program collapsed the six intervals to three before analyzing the data.

Results

Location of Subjects after Release in Spring

In 1985, following release of 120 juncos on 19 and 23 Feb., we made 132 captures of juncos at the capture sites (on 10 days between 27 Feb.—19 Mar.). None was of an experimental bird. We also trapped and netted (on three days between 20 Mar.—1 Apr.) at the confinement-release site, where 22 of 61 captures of juncos were of experimental birds (19 different individuals, 16 % of the number released).

In 1986, following release of 172 juncos on 20 Feb., we caught birds on 5 days (3—12 Mar.) at the capture sites. Among 52 captures there, none was of an experimental bird. In contrast, of 259 captures (on 6 days between 26 Feb.—16

Mar.) at the confinement-release site, 185 were of experimental birds (73 different individuals, 42 % of those released).

In 1987, following release of 168 juncos on 21 Feb., we caught birds (on 13 days between 22 Feb.—20 Mar.) at the capture sites. Among 112 captures of juncos there, one was of an experimental bird that had homed a distance of 12.8 km. We also caught juncos (on 11 days between 3—30 Mar.) at the confinement-release site. Of 260 captures, 139 were of experimental birds (72 different individuals, 43 % of those released).

Returns in the Following Winter

From the total of 608 subjects, 24 individuals (3.9 %) were caught in years following those in which we held them (Table 1). Of these, four returned to the confinement-release site and 20 to the capture site (all five locations). There was no significant sexual difference in return rate (Fisher's exact probability = 0.381), and we pool the sexes in further presentation.

Table 1: Numbers of young juncos that returned in the next year (Exp. 2, all years pooled) either to the capture site or the confinement-release site, according to date of confinement and place of return

	Date						Total
	1—10	December 11—20	21—31	1—10	January 11—20	21—31	
Held	121	87	100	60	123	117	608
Returned to							
capture site	0	3	3	1	6	7	20
release site	0	1	1	0	1	1	4

The earliest capture of an individual that returned next year to the capture site was on 15 Dec., the latest on 30 Jan. In the test for a correlation between return to the capture site and date of capture there in the preceding winter (604 subjects, i.e. excluding the four birds that returned to the confinement-release site), χ^2 associated with logit analysis = 5.21, $df = 2$, $p = 0.074$. Thus there tended to be a relationship between date of capture-confinement and probability of return.

Both among juncos that returned to the capture site and to the confinement-release site were individuals that had remained at the confinement-release site after being let go in the preceding spring, i.e., that had not homed. Two juncos that we caught and displaced late in the capture period (on 16 Jan. and 24 Jan.) nevertheless returned to the confinement-release site instead of the capture site, which presumably they had occupied since completing autumn migration.

There was no apparent relationship between distance separating the confinement-release site from the capture site and probability of return to one site or the other (data not shown). Whether attachment was to the confinement-release site or the capture site, it apparently was life-long, as we have found to be true of juncos in nonexperimental situations: individuals that return once to the previous

year's winter site continue to do so in future years at a rate equal to the annual survival rate (KETTERSON & NOLAN 1982).

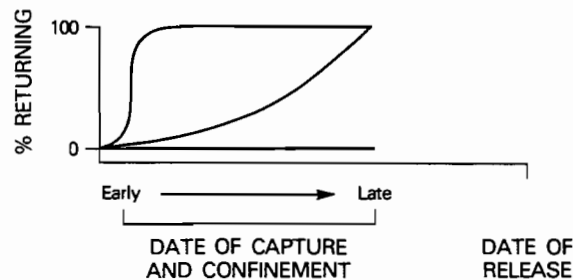
Discussion

Young displaced juncos that we released in late winter rarely homed to the capture site before migrating northward (one observed case among 460 subjects). Instead, a large proportion (36 %) remained at the point of release, all for at least 10 days. Failure to home seems more likely to be the result of absence of motivation than lack of capacity, as suggested by the fact that most birds that returned next year were caught on their original capture sites. These results closely resembled the findings of RALPH & MEWALDT (1976) for *Zonotrichia* sparrows (see also BENVENUTI & IOALÉ 1980).

Because homing after release was rare, the attachment to the capture site of juncos that returned there next year must have formed before they were confined. Although the statistical correlation was nonsignificant, young juncos that lived free at the capture site until mid- and late Jan. were somewhat more likely to form an attachment to that site than were those confined earlier (Table 1). However, attachment to the confinement-release site did develop even in some individuals that were not taken from the capture site until late winter. Hence the timing of completion of attachment was variable.

What do these results reveal about the process underlying formation of a site bond? Fig. 1 models three possible results of a staged-delayed-release experiment like Exp. 2. The left-hand, rapidly rising curve depicts the situation in which birds return to the capture site even if they had only minimal opportunity to live free there after completing migration; this is consistent with rapid learning during an early-winter sensitive phase. In the horizontal curve, no birds return to the capture site regardless of how long they lived free there. Assuming that they return to the displacement-release site, this curve is consistent with rapid learning late in winter. The gradually rising concave curve represents the case in which probability of return increases with length of time the individual lived free before capture. (Variations can be imagined, e.g., a sigmoid curve representing a normal distribution of the dates at which site attachment is completed.)

Fig. 1: Three possible data sets from a staged-delayed-release experiment. Returns of displaced birds to the capture site vary according to date of capture. Sigmoid curve: returns when site attachment is a rapid process occurring in early winter. Flat horizontal curve: returns when site attachment is a rapid process occurring in late winter. Concave curve: returns when site attachment is a gradual process, varying in duration among individuals; but see text for an alternative possibility



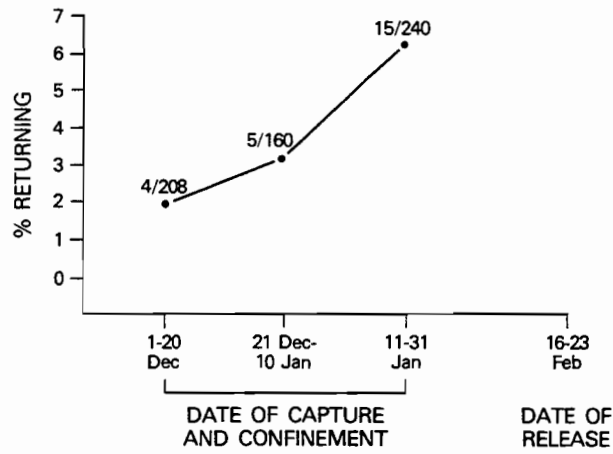


Fig. 2: Returns of young juncos to their capture site in Exp. 2. Data from Table 1 are grouped into three 20- or 21-day-long capture periods

The data in Table 1 do not fit the left-hand curve or the horizontal curve, and we conclude that site attachment in young juncos does not occur rapidly, either in autumn-early winter or in spring (see SCHWARTZ 1963). Rather, attachment forms at different dates for different individuals, which is consistent with the view that varying, gradually accumulating experiences are the basis for the young junco's site fidelity (compare Fig. 1 with Fig. 2). Considering that winter home ranges differ in quality and that dominance hierarchies are a prominent feature of the junco's winter social organization (SABINE 1959; BALPH 1977; KETTERSON 1978), we would expect individual variation in the kind and timing of experiences responsible for site attachment.

Nevertheless, for two reasons our data leave open the possibility that attachment occurs rapidly and during a sensitive phase, but at different dates for different individuals. First, not all young winter residents arrive at Bloomington on the same date (NOLAN & KETTERSON 1990). If the process of attachment is triggered by arrival at the winter site, individual differences in arrival date could cause variation in timing of attachment. On the other hand, it is unlikely that our site-faithful juncos varied as greatly in arrival date as they did in capture date; we captured site-faithful young over a 47-day period (15 Dec.—30 Jan.), whereas about 90 % of winter-resident young arrive in Bloomington in Nov., most of them in the last half of that month (NOLAN & KETTERSON 1990). A second possibility, consistent with the existence of a sensitive phase for site attachment, is based on the fact that junco broods leave the nest over a considerable range of dates (PETERS & BURLEIGH 1951; SQUIRES 1952; HOUSTON & STREET 1959; GABRIELSON & LINCOLN 1959; pers. obs.). If a sensitive phase begins at a certain age, variation in age could cause variation in timing of site attachment. However, in a number of bird species, and possibly in juncos, the developmental processes of late-hatched individuals are accelerated; as a result their schedules tend to catch up with the schedules of early-hatched conspecifics (see GWINNER 1986 for review). In such species the variance in date of life-history events such as migration can be much smaller than the variance in date of hatching.

If learning is gradual and the existence and timing of attachment vary according to experience, late-winter experience may be especially important for some individuals. This is suggested by the return to the confinement-release site, i.e., the aviary, of the two juncos not displaced until after mid-Jan. The results of Exp. 1 also may support this possibility: the fact that all subjects were alike in being free at their capture sites in Mar. may account for the absence of correlation between date of capture-confinement and return the following winter.

Future research on the general subject of this paper would be most productive if it employed the staged-delayed-release method on a strongly site-faithful species that raises a single brood during a short breeding season and that migrates more synchronously than do juncos (NOLAN & KETTERSON 1990). Whether or not experiments on such a species indicate that an imprinting-like process is the basis for winter-site fidelity, experiential factors will underlie the attachment. Further experiments could explore the critical stimuli and vary experiences by manipulating attributes of the site, e.g., structure of the habitat, population density, and level of food abundance.

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