

Site Attachment and Site Fidelity in Migratory Birds: Experimental Evidence from the Field and Analogies from Neurobiology

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1 Introduction

In this chapter we review briefly what field experiments have revealed about the formation of site bonds by avian migrants and, in so doing, consider whether it is fruitful to continue the practice of attributing site attachment to an imprinting-like process. We then refer briefly to recent findings in the neurobiology of recognition of objects and sites in three areas of investigation: filial imprinting, relocation of food by food-caching birds, and homing by pigeons. We suggest that analogies between these findings and site recognition in migratory birds may indicate new directions for research. These suggestions are speculative because current knowledge is slim; we hope the speculations may have heuristic value.

2 Site Attachment and Site Fidelity

2.1 *Natural History of Site Attachment*

Understanding of the development of site attachment in the migratory bird is incomplete and derives primarily from banding studies, supplemented by limited experimental work (see Baker 1978 for summary; Sokolov 1976, 1982, 1984, 1986, 1988). Newly independent birds are thought to disperse locally, to explore their surroundings, and perhaps to select potential breeding sites for the following spring. The distance dispersed prior to this choice, regardless of whether the choice is made in the bird's first autumn or in spring, is thought by many (e.g., Shields 1982; Greenwood 1987) to be determined by natural selection so that it balances the disadvantages of mating with close relatives and the advantages of mating with individuals whose genetic makeup has been molded by similar selective pressures. In general, the distance is greater for female birds than for males (e.g., Gauthreaux 1978; Greenwood 1980).

The individual then makes its first autumn migration, settles in a suitable winter site, becomes familiar with its surroundings, and, in many species, forms a bond that will cause it to return in succeeding winters (e.g., Ralph and Mewaldt 1975; Ketterson and Nolan 1982; Terrill, this Vol.). From this time on the

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migrations of site-faithful individuals are between known breeding and non-breeding areas. Additionally, in some species individuals are caught at the same stopover locations in successive migrations, indicating familiarity with migratory pathways and fidelity to sites along the way (Nolan and Ketterson, in preparation). The details of the development of bonds to seasonally occupied locations surely vary widely among migratory species, just as life history traits and ecology vary widely.

2.2 Terminology

We use the term site attachment for the processes leading to formation of a bird's preference for a location. These processes, which involve learning and memory (e.g., Löhrl 1959; Serventy 1967; Wiltschko and Wiltschko 1978; Berndt and Winkel 1979), result in the tendency to confine activities to a restricted location, and they occur in both sedentary and migratory species. It seems useful, therefore, to use a separate term for the expression of the preference by the free-living migrant, and we define site fidelity as the act of a migrant in returning to a location occupied in an earlier season or year.

2.3 Components of Site Attachment/ Site Fidelity

Site fidelity implies not only that the migrant has learned the attributes of the site; it also requires the motivation and the ability to return, including the abilities to orient and to recognize the site upon arrival. These abilities may exist in sedentary species as well (Wiltschko and Wiltschko 1978; Nolan et al. 1986), but rarely have cause for expression. In any case, in migrants, recognition of the site to which there is a bond apparently interacts with the migratory physiological state and leads to the termination of that state (Ketterson and Nolan 1987a).

While the orientational component has received much productive attention, almost nothing is known of the recognition stage, i.e., what the relevant learned attributes of the site may be or how perception of them influences physiology. Some have proposed that animals develop an integrative cognitive map and possess the capacity to compare current environmental input to that internal representation (O'Keefe and Nadel 1978; Bingman 1990). In that view, recognition of the site upon arrival there might consist of matching the perception of spatial distribution of the landmarks with the memorized cognitive map. Alternatively, the animal might simply respond to one or two key stimuli as indicators of home. What the landmarks or stimuli might be is not known, although they are often tacitly assumed to be visual and there are some experimental data to support that view (Schmidt-Koenig and Walcott 1978).

2.4 Field and Laboratory Experiments Investigating Site Attachment and Site Fidelity

We are aware of two experimental approaches to the investigation of site attachment and thus site fidelity. The first, which we term staged release, is to displace birds at different stages of development (ages) and determine the correlation between their age or experience when displaced and the site to which they return, either in the year of displacement or later (e.g., Löhrl 1959; Ralph and Mewaldt 1975, 1976; Benvenuti and Ioalé 1980; Sokolov 1984). This approach has so far contributed little to identifying the cues necessary for recognition but has been quite useful for identifying the time or age at which attachment takes place.

The second method is to expose birds to a location that was their destination in a previous migration and to observe how this exposure affects their current season's migratory state (Stimmelmayer 1932; Gwinner and Czeschlik 1978; Ketterson and Nolan 1983, 1987a,b, 1988; Nolan and Ketterson, in press). If birds released or held at their migratory destination fail to migrate when it is time to do so, or to fatten and show Zugunruhe, this can be taken as evidence that they recognized the site. This approach, undertaken on caged birds, might ultimately prove amenable to cue manipulations. As yet, however, we know of only one attempt (Gwinner and Czeschlik 1978) to alter systematically the cues available during the phase in which migrants learn a site (acquisition stage), and we are aware of no manipulations during the recognition stage. The results of the lone experiment were negative, quite possibly because caged birds cannot learn the cues necessary for site attachment and recognition (Löhrl 1959; Berndt and Winkel 1979; Sokolov 1984; Nolan and Ketterson, in press).

A series of experiments in which, prior to autumn, we exposed both caged and free-living (released) dark-eyed juncos (*Junco hyemalis*) to their autumn migratory destination has been reviewed by us (Ketterson and Nolan 1988). Therefore, we present here only the results of a more recent study on indigo buntings (*Passerina cyanea*). Sniegowski et al. (1988) and Sniegowski (unpublished data) caught male buntings on their breeding territories, held them until the following spring, and then released them on their territories at a date when migration was just beginning among free-living conspecifics wintering far to the south. Controls were transported and released 1000 km to the south. If the birds released on territory recognized the site, and if recognition is sufficient to terminate migration, the experimentals would be expected to delete migration from that year's cycle, whereas the controls would be expected to migrate home. If the buntings released on territory did not remain there, then it might be concluded either that they did not recognize the site or that recognition could not override the seasonal physiology of migration. The results (Table 1) are equivocal but suggestive. Some of the buntings released on their territories remained (cf. the similar result in an early experiment by Stimmelmayer 1932, with one bluethroat, *Erithacus svecica*, and one chiffchaff, *Phylloscopus collybita*). Furthermore, some released to the south returned. However, most individuals in both treatment

Table 1. Behavior of indigo buntings released prior to initiation of migration, at and away from their migratory destinations^a

Release site	Number released	Remained at home	Migrated home	Unaccounted for
Home-Indiana	20	7	—	13
Away-Florida	20	—	8	12

^a Combined data for 1985, 1986, from Sniegowski et al. (1988) and unpublished data by Sniegowski.

groups were unaccounted for, and it is possible that those released on territory may have migrated northward.

We conclude from results of the second experimental approach that, when migrants are exposed to their perennial migratory destination at the beginning of the migration season, at least some individuals recognize the site and this recognition overrides migration. However, further progress probably will require a system that can be brought under laboratory control, although we have just acknowledged the difficulty of controlling in the laboratory a phenomenon expected only in free-living birds [but see the laboratory studies of Glück (1984) and Roberts and Wiegl (1984) on habitat preference and of Hess (1973) on environmental imprinting].

3 Timing of Site Attachment and the Imprinting Model

Site attachment appears in certain ways to be analogous to imprinting, and imprinting is sometimes invoked in accounting for site attachment (Löhrl 1959; Sauer 1967; Serventy 1967; Ralph and Mewaldt 1975; Berndt and Winkel 1979; Sokolov 1984). Imprinting is usually described (e.g., Bateson 1979) as a special kind of learning in which (1) the information that is acquired restricts future preference and (2) acquisition occurs rapidly during a critical or sensitive period or phase. Some definitions require that the learning be accomplished without reinforcement and that the preference be irreversible or be retained for a long time without intervening practice.

Most research on site attachment that has drawn inspiration from imprinting models has focused on the timing of attachment, with at least an implicit expectation of finding a sensitive period. Existence of such a period is traditionally demonstrated with data graphed as an inverted U- or V-shaped curve (Fig. 1A). Subjects are exposed to a stimulus over a range of times and later tested to determine whether they established a preference for the stimulus. If exposure is before or after the sensitive period, no preference is exhibited. Only exposure during the sensitive period establishes a preference, which is graphed as the peak of the curve.

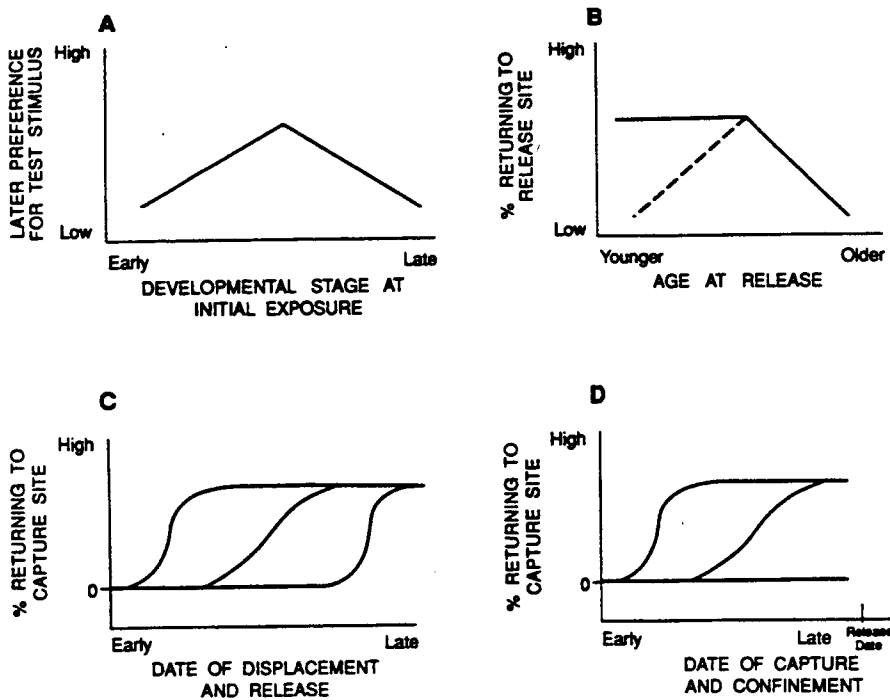


Fig. 1A-D. Expected results of staged-release experiments under various hypotheses and experimental designs to investigate timing of learning. **A** Classical evidence for a sensitive phase in imprinting. **B** Expected results in a staged-release experiment such as Löhrl's. *Solid line* shows observable results; *dashed line* the results necessary to demonstrate a sensitive phase. **C** Expected returns to capture site when displacements are at various dates and subjects are released immediately. In *left-hand curve*, a brief imprinting-like process occurs early in the season; in *right-hand curve* it occurs late in the season. In *central curve*, learning is by a gradual, individually varying process or possibly by an imprinting-like process whose date varies among individuals. See text. **D** Expected returns to capture site in a staged-delayed-release experiment. Captures are at various dates, and subjects are displaced and held until late in the season, then released simultaneously at the displacement site. *Left-hand rising curve* shows returns to the capture site if a brief imprinting-like process occurs early in the season. *Bottom horizontal curve* shows returns to the capture site if a brief imprinting-like process occurs late in the season. The *right-hand rising curve* shows returns to the capture site if learning is gradual and date of its completion varies among individuals

3.1 Attachment to the Natal Site

In field experiments to determine the timing of attachment to the natal site, individual birds are released at various ages and their later tendency to return is monitored. The problem with this method, however, is that the expected result is not an inverted U. The reason is that birds released prior to the start of the putative sensitive period will, if they do not disperse, still be present at the beginning of the sensitive period and therefore should return at the same rate as birds released when the period begins. Only individuals released after the sensitive period is

complete would be expected to form no preference (Fig. 1B). Thus, this sort of experiment cannot reveal the existence of a sensitive period, although it can produce data consistent with the concept. In a field study, to produce the inverted U required for a rigorous demonstration of imprinting, birds would have to be released at a first site at a range of developmental stages, be recaptured and held after a period in which they lived free, and finally displaced and released at a second site so that those with a preference for the first site could be observed to express it. This experiment is so difficult that we do not expect it to be made.

The curve in Fig. 1B is very similar to a curve of the results in the classic experiment of Löhrl (1959), whose young collared flycatchers (*Ficedula albicollis*) were released at different ages at a location 90 km distant from their rearing site (which was not the natal site). Individuals released prior to or early in post-juvinal molt returned to the displacement site, whereas those that were released late in molt or after molt was completed (the stage at which autumn migration begins) did not return (Fig. 2). The few similar studies since Löhrl's (e.g., Serventy 1967; Berndt and Winkel 1979) have confirmed his finding that attachment to the natal and/or rearing site involves learning: birds transported when sufficiently young return to the displacement site. But with the possible exception of Serventy's work (1967), we are aware of no further demonstration of the termination of a phase in which learning occurs. We therefore suggest that there is little evidence to justify the general conclusion that natal site attachment is an imprinting-like process. The data seem to point just as consistently to a process of gradual learning, including exploration and expansion of a familiar area (Baker 1978), that culminates in attachment.

3.2 Attachment to the Winter Site

Investigators have also considered whether an imprinting-like process may account for attachment to the wintering site (Ralph and Mewaldt 1975, 1976). In these staged-release experiments marked birds are displaced at various dates in

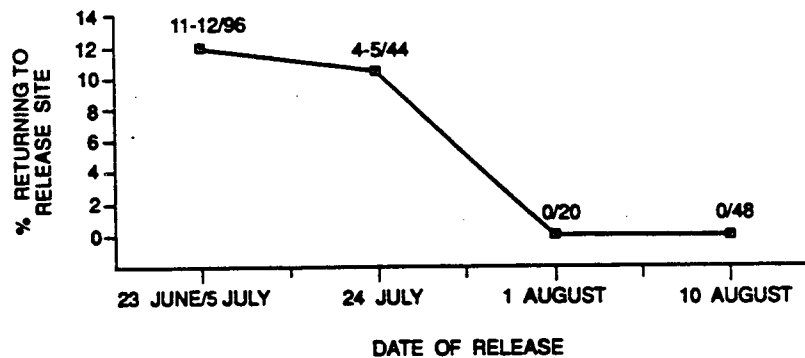


Fig. 2. Returns of collared flycatchers hand-reared away from natal site, displaced at various stages of development, and released at a distance from rearing site (After Löhrl 1959; cf. Fig. 1B)

their first winter and the percentages returning next winter to the home site are analyzed in relation to date of displacement. Ideally for such a study, all birds would remain at the release site until migrating northward in spring (i.e., would neither home to the capture site nor settle in some unknown place), and the survivors would indicate by their choice of the following winter's site whether they had become attached to the capture-home site or the displacement site. Figure 1C depicts the expected results, first, under the hypothesis that site attachment occurs rapidly during a sensitive period either early in winter (left-hand curve, Benvenuti and Ioalé 1980) or late in winter (right-hand curve, Schwartz 1963) and, second, under the alternate hypothesis that learning is gradual and varies with individual experience (middle curve). In all three possibilities, birds displaced prior to attachment fail to return to the capture-home site and those displaced after attachment return to that site. We emphasize, however, that the middle curve in Fig. 1C could also be generated by an imprinting-like process. If learning is rapid and precisely timed during a sensitive period in each individual, but the date of learning varies among individuals, the behavior of the population might be best represented by a normal distribution with the peak in mid-winter; the curve would look the same as if learning were gradual and variable. This kind of individual variation could be produced if members of the population differed in age by, say, 2 months according to whether they hatched during the preceding breeding season in early broods, mid-season broods, or late broods. One point of Fig. 1C is that these different possibilities are difficult to distinguish experimentally.

An experiment like that depicted in Fig. 1C was carried out by Ralph and Mewaldt (1975, 1976), who transported crowned sparrows (*Zonotrichia* spp.) various distances from their winter sites. The rate of return next year by young sparrows to the capture site varied according to date of displacement: those displaced prior to mid-January were less likely to return, and site attachment was believed to have occurred by mid-January. As the authors pointed out, birds displaced early in winter must survive for a longer period before their return can be observed next year; that is, the probability of mortality in the interval between displacement and the following winter presumably would be positively correlated with the length of that interval.

The experiment depicted in Fig. 1D is a variation on Fig. 1C and was designed to overcome the facts that transported birds do not necessarily remain at the release site until they migrate and that variation in length of the interval between release and return may affect the numbers that can be expected to return. In this staged-delayed-release design, birds are captured over a range of dates, displaced to and held at a second site, and released simultaneously at the displacement site late in winter, in time to migrate. This treatment prevents homing and also eliminates variable mortality after capture, whatever the date of capture. Next winter, return is monitored at both the capture site and the displacement site. If attachment occurs rapidly either early in winter or late in winter (Schwartz 1963), all returns should be to one site, the capture site or the displacement-release site, respectively. If learning occurs gradually, the percentage of birds returning to the capture site should be greatest among individuals

captured latest, and some individuals might be expected to return to the displacement-release site.

Results of such an experiment appear in Fig. 3 (Nolan and Ketterson, in press). Dark-eyed juncos caught throughout December and January were displaced to an outdoor aviary surrounded by suitable junco habitat; they were released there in late winter. Intensive efforts in the following autumn and winter, both at the original capture site and at the aviary release site, yielded few returns of birds caught at any date, but there were two notable results. First, juncos caught late in winter tended to return at a greater rate than those caught earlier. When the data are analyzed with the capture period divided into thirds, chi square = 4.72, $df = 2$, $0.10 > p > 0.05$. Second, a few individuals caught during all thirds returned to the displacement site, indicating that the timing of site attachment was highly variable. Thus, whereas an individual caught as early as 12 December exhibited fidelity to the capture site, another caught as late as 24 January returned to the displacement-release site. (A young junco not included in this experiment was captured on 5 February, displaced to the aviary, and released there on 21 February; it returned next winter to the aviary.)

To summarize, it seems appropriate to ask whether the tradition of using the language of imprinting to describe site attachment should be continued. To be sure, information stored during site attachment can be retrieved after a long interval of no practice, but it seems to us that the evidence for a sensitive period — the most important criterion for imprinting — is slim at best. In order to study further the question of the relationship between imprinting and site attachment we need a study system with greater resolving power.

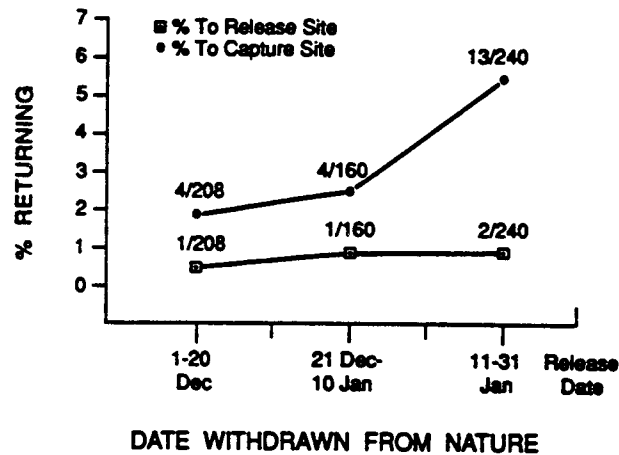


Fig. 3. Returns of young juncos in a winter staged-delayed-release experiment. Birds were caught at various dates in winter, displaced and held until late winter, then released simultaneously at the displacement site (cf. Fig. 1D)

4 Neural Bases of Behaviors Somewhat Analogous to Site Fidelity

Recent advances in understanding of the neural bases of three kinds of avian behavior should interest students of site fidelity: filial imprinting (summarized in Horn 1985), food-caching (Sherry and Vaccarino 1989; Krebs et al. 1989), and pigeon homing (summarized in Bingman et al. 1984, 1985, 1988, 1990). Each behavior involves recognition and thus has a component that is at least superficially analogous to a component of site attachment and site fidelity. Further, thus far at least, the behaviors have proved amenable to study. Space limitation permits only brief reference to this work and necessarily requires that we oversimplify, but we point out that two themes emerge. First, particular regions of the brain have come to be associated with a bird's ability to learn the attributes of, and later to recognize, significant places or objects. Second, this neurally localized ability to recognize can be uncoupled from other abilities, including the ability to learn tasks that require the very behaviors (motor patterns, visual discriminations) ordinarily associated with recognition.

4.1 Filial Imprinting

Filial imprinting occurs when young birds (e.g. *Gallus gallus*) follow their mother or some artificial substitute, with the well-known result that an attachment is formed to the object followed (this subsection is drawn from Horn 1985). Imprinting is demonstrated when the chick subsequently shows a preference for the followed object over some other potential imprinting stimulus. This preference requires that the chick recognize the stimulus on which it trained.

During imprinting a neural representation of the imprinting stimulus is stored in the brain, and autoradiography and lesioning implicate the intermediate and medial part of the hyperstriatum ventrale (IMHV) of the forebrain as the region in which storage takes place. When the IMHV is missing, a chick cannot acquire a preference. Further, when this region is lesioned in chicks that already have acquired a preference through imprinting, under some circumstances they can no longer recognize the imprinted stimulus.

One of Horn and his associates' most interesting findings is that it is possible to dissociate (uncouple) recognition of a stimulus from associative learning of that same stimulus. Chicks respond to potential imprinting stimuli as reinforcers. A chick placed in a cage with two foot pedals, only one of which will activate a view of an imprinting stimulus, will quickly learn to press the pedal that activates the view if it finds the view rewarding. The capacity to learn this task is unaffected by lesions to the IMHV. However, when these same lesioned chicks are compared to controls in their *preference for* the very stimulus they just worked to see, only the controls exhibit the preference. In other words, the IMHV is not necessary to learning a task that permits a chick to look at a stimulus it finds rewarding, but it is necessary to the chick's later ability to recognize that thing. This dissociability of recognition from task learning is the kind of observation that is leading neurobiologists to invoke the existence of multiple memory systems (Sherry and Schacter 1987).

4.2 Caching

In the last decade many studies have documented the memory capabilities of food-caching birds, some of which can retrieve their caches after several months (e.g., Kamil and Balda 1985; Balda et al. 1987). Two recent investigations have linked these capacities to a specific region of the brain, the avian hippocampus (HP). In comparisons within families, species with the greater tendency to store and recover food have larger hippocampal regions (Sherry et al. 1988; Krebs et al. 1989), and investigation of the impact of HP aspiration on cache recovery in chickadees (*Parus atricapillus*) shows that subjects lose their capacity to remember (recognize visually) the location of cache sites after aspiration (Sherry and Vaccarino 1988). These chickadees are still motivated to search and they retain all the motor and visual discriminatory abilities to do so after aspiration, but they apparently lack the ability to recall the spatial relationship between fixed feeding sites.

Whether these findings will prove relevant to site attachment is problematic. On the one hand, the task facing a bird attempting to recover stored food might be seen as involving components similar to those in the task confronting a bird about to migrate to a previously learned site: motivation to return, orientation, and recognition of the site upon arrival. On the other hand, at least two differences between food retrieval and site fidelity suggest underlying differences in the neural processes involved. In using food-storing memory, the bird makes only one visit to the cache and may learn only a single cue by which to recognize it, whereas site attachment is almost surely not based on one brief episode and, correspondingly, the memory is probably a composite of cues learned during various experiences. Further, for efficient food retrieval cache sites must either be forgotten once a seed has been retrieved or, if memory continues, the cache must be avoided unless or until it is used again (Sherry and Schacter 1987). Site fidelity is unlikely to involve such "programmed forgetting."

4.3 Orientation and Homing

Results of studies by Bingman and associates (1984 summarized in Bingman et al. 1990) are consistent with the view that the avian hippocampus plays a necessary role in spatial recognition by homing pigeons (*Columba livea*). When HP-ablated pigeons are released 50 km from home, their ability to orient as well as controls depends upon the mode of orientation that they use, and they exhibit markedly reduced ability to reach home. When they have previously been familiar with landmarks at the release site and are forced to rely on visual recognition as their homing mechanism, homing is much impaired. Furthermore, when released nearer home, they evidently fail to recognize their home loft when in its vicinity. After postoperative retraining, however, many of the normal orientational and recognition abilities are restored.

According to Bingman (personal communication), a speculative application of these results to a migratory, potentially site-faithful bird would be as follows:

An individual that was caught in winter, subjected to hippocampal ablation, and released would have the opportunity to relearn its winter site after release but not to relearn its breeding site. If it migrated and succeeded in reaching its breeding site (and the pigeon results suggest that it might succeed), it probably would not recognize the site and so might not pass out of the migratory state. However, the following autumn it would be expected to recognize its winter site, again assuming that it reached that destination.

5 Summary and Further Speculation

There seems little reason to expect a priori that the relevant characteristics of a breeding or winter site would be stored for the long term in the same location in the brain as the quickly learned representation of a followed object. Rather, it is intuitively more appealing to describe the process of recognizing home after migration as one of matching current environmental input to a stored cognitive map. The implication of the hippocampus in recalling or recognizing food locations is provocative, but we have pointed out apparent dissimilarities between what is involved in the process of remembering the locations of a food cache and a home range. Further, the indication that the hippocampus is not necessary to the reacquisition of many spatial abilities in pigeons considerably obscures the importance of that structure. Whatever the relevance of these neural studies for site fidelity, it seems clear that we need to find a tractable study system that will permit us to dismantle the neural and behavioral components of this fascinating animal ability, preferably first in the laboratory and then in the field.

Acknowledgments. For kind assistance in the preparation of the manuscript we thank S.B. Robbins and L. Wolf. For generously sharing their work prior to publication we thank D.F. Sherry, V.P. Bingman, and P.D. Sniegowski. For stimulating discussion and helpful suggestions we thank G. Ball, W. Timberlake, A. Kamil, R. Wiltschko and R. Suthers. Aspects of our own research reported herein were supported by NSF DEB-81-10457 and BNS-83-15348 and by Indiana University's Office of Research and Graduate Development.

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