CHAPTER 5

INFORMED DISPERAL
Prospecting by Birds for Breeding Sites

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1. INTRODUCTION

The quality of a bird's breeding site is a primary determinant of its success or failure to reproduce there. We expect birds to devote considerable effort to acquiring accurate information about potential locations before finally selecting a breeding site (e.g., Wians, 1976; Lack, 1971; Howard, 1920). The great mobility of birds strengthens this expectation, which is also reinforced by the accumulating evidence of avian cognitive abilities (e.g., Cook et al., 1997; Cook, 1993). In this chapter...
we review theoretical considerations and empirical evidence that birds gather advance information about possible breeding sites within a general area before settling to breed within that area. This gathering process, which we term *prospecting*, has received little systematic attention despite its potential interest and its obvious importance for individual fitness, population dynamics, and distribution.

We envisage prospecting as more refined in scale than either the process of selecting a general area within the breeding range or of choosing habitat characteristics that are appropriate for the species (e.g., forest as opposed to meadow). The first potential occasion for prospecting is the period, or some part of it, before the initial breeding attempt of life, and similar occasions arise before every later attempt, whether or not the individual chooses to relocate or remain on its most recent breeding site. We see no difference in principle between prospecting by sedentary birds and by migrants, once the latter have returned to their portion of the breeding range. Migrants, however, may have less time available to prospect, and this may raise the cost of the behavior and thereby affect its extent and nature. Similarly, prospecting by birds that breed in the year following hatching would not appear to differ from birds whose maturation is delayed, except the latter have more time to search for the initial breeding site. Again, this may affect the cost:benefit ratio of the behavior and therefore the behavior itself.

A threshold question in analyzing prospecting is this: How does the field observer recognize prospecting? Any bird moving about in its general breeding area is probably acquiring and storing information that could affect the choice of its next breeding site, even though all the observer may see is, for example, foraging. Therefore, we exclude from our definition of prospecting all behavior that takes place within the individual's current or most recent breeding site, even though the bird is likely to be accumulating information that will lead it to accept or reject that site for future breeding attempts. On the basis of our review of the literature (see Section 3., below), we confine our definition to include three categories of behavior: 1) all activities in which a bird engages, while not on its current territory, that would be recognized as species-typical behavior preparatory to nest-building or territory establishment; 2) any activity by an individual at a location that is not its breeding territory, if the individual later returns to that location to breed; and 3) the temporary occupation of a site on which the individual—usually a male—behaves territorially (for hours or even weeks) before disappearing, still unmated. We include this final category because a bird can examine multiple locations before selecting one of them for breeding.

Researchers working on Black-legged Kittiwakes (*Rissa tridactyla*) identified three types of prospectors (Cadiou et al., 1994; Danchin et al., 1991; Monnat et al., 1990): 1) juvenile or immature birds (i.e., individuals that have never bred); 2) failed breeders, which observers often identify incorrectly as nonbreeders (e.g., it is usual to find that a female new to a site in mid-season has a brood patch, which indicates she has bred previously); and 3) true nonbreeders (i.e., birds that have bred in previous years but have not mated during the current year). Prospecting by successful breeders also occurs (e.g., Jackson et al., 1989); such prospecting would be particularly useful when temporal variability in habitat quality is high and prior reproductive success does not predict success in the future.

Prospecting for breeding sites has been observed in marine invertebrates (Doyle, 1975), fish (Armstrong et al., 1997; Hoelzer, 1987), and mammals (O'Donoghue and Bergman, 1992; Waterman, 1992; Woollard and Harris, 1990); but it has been described most frequently in birds. One of the first discussions of this behavior we have found concerned waterfowl. Hochbaum (1946) inferred the existence of prospecting for breeding sites from observations that newly created waterfowl breeding areas were rapidly colonized. He argued this could occur only if birds explored for potential breeding areas and used that information later. He further noted variation among species in their tendency to prospect, pointing out that puddle ducks (e.g., tribe Anatini) were more likely than diving ducks (e.g., tribe Aythyini) to take rapid advantage of newly available habitat. Hochbaum (1946) explained this difference affected the speed with which populations recovered from low numbers, with species that prospected recovering more quickly. Although this type of observation was common in the wildlife literature (e.g., Leopold, 1933), we are uncertain as to when the concept of prospecting was formalized and applied more generally.

In this chapter we first (Section 2.) review the few existing models of avian prospecting and also argue that models of other kinds of spatial behavior might contribute to improvement of models of prospecting. We then (Section 3.) present the results of a literature review, which provides us with an inventory of the behavior patterns we interpret as prospecting. Next (Section 4.), we consider what kinds of information a prospecting bird might find useful and cite evidence that some species do in fact acquire and use such information. We follow this with analysis of dispersal patterns of birds (Section 5.); these patterns may determine, or be determined by, the opportunity for and advantages of prospecting.

In Sections 6. and 7., respectively, we review the literature on prospecting by first-time breeders and by experienced breeders. We
then consider the possible mechanisms birds may use in gathering, integrating, and exploiting information gained by prospecting (Section 8.) and the relevance of prospecting to human efforts to conserve bird species (Section 9.). We conclude (Section 10.) with suggestions for future research.

2. MODELS OF SPATIAL BEHAVIOR

Animals regularly gather information that they use when determining their distribution in space (e.g., they monitor mate availability, Colwell and Oring, 1989). The decision-making processes and their possible results have been a fruitful ground for modeling behavior in many areas (e.g., foraging and mate choice), but less attention has been given to prospecting for breeding sites. A reason for this neglect, we believe, is the practical difficulty pointed out above: the problem the observer has of identifying prospecting in the field. Nevertheless, the study of prospecting can profit from consideration of ideas advanced in other areas. Foraging models (Yoccoz et al., 1993; Valone and Giraldeau, 1993; Krebs and Inman, 1992; Pöysä, 1992; Valone, 1989; Bernstein et al., 1988; Shettleworth et al., 1988; Stephens, 1987; Tamm, 1987; Abrahams, 1986; Clark and Mangel, 1984; Kiester and Saltkin, 1974) and models of mate choice or territory selection (Danchin and Wagner, 1997; Ens et al., 1995; Parker and Sutherland, 1986; Fretwell and Lucas, 1970; Orians, 1969; Verner and Willson, 1966), especially those dealing with patchy environments, take into account that individuals gather information. Gathering information on the environment also can be used to decrease the probability of predation (e.g., Clarke et al., 1993; Isbell et al., 1990), to monitor food sources (Benedix, 1993; Meretsky and Snyder, 1992; Rodgers, 1990), and to search for extra-pair copulation opportunities (e.g., Wagner 1993, 1997; Wagner et al., 1996; Hanski, 1992; Hanski et al., 1992; Reynolds and Linkhart, 1990; Møller, 1987). In this context, theoretical models of prospecting behavior are important to determine conditions in which information gathering may be adaptive and to examine the effects of such behavior on the distribution of individuals in the environment.

2.1. Models of Prospecting

There are now several models of prospecting behavior. Baker (1978) developed a general model to predict when an animal should "migrate," a term that he defined broadly to include any nonaccidental movement including a one-way movement, e.g., from one perch to another, from the breeding site to the winter site, etc. The model's scope thus includes the decision to leave any previously-occupied location in favor of finding a breeding site, and it predicts when a prospector should terminate prospecting and decide to settle on a breeding site. Baker balances the decision whether or not to move (including to continue searching) between the suitability ($h_i$) of the occupied "habitat" ($H_i$) with the suitability of another habitat, discounted by a migration factor ($M$). Habitat suitability is a function of expected lifetime reproductive success. For a species capable of exploring an environment (Baker's "exploratory-removal migration" sequence), an animal should move from $H_i$ when

$$h_i < E_{sc},$$

(1)

where $E_{sc}$ is the mean expectation of reproductive success that would result from moving, i.e.,

$$E_{sc} = h_{max}M_{sc}.\quad (2)$$

During exploration, $h_{max}$ is the maximum suitability of the best habitats encountered (i.e., those offering the highest expected reproductive success), and it increases over time (i.e., as more sites are sampled, better sites are found). $M_{sc}$ is a migration factor, with a maximum value of 1.0 at time $t_o$ that declines monotonically over time spent prospecting. The shape of the decline curve varies according to the cost of exploration and the type of exploratory behavior exhibited (Baker, 1978:64). As a consequence, $h_{max}M_{sc}$ peaks at some intermediate search time, and prospecting stops when the animal settles in the habitat with the highest suitability encountered.

Ketterson and Nolan (1983) criticized Baker's (1978) model from the perspective of differential migration in birds, i.e., round-trip migration in which some population class(es), such as a sex class, migrates a greater mean distance than some other class(es) (see Cristol et al., this volume). Their primary concern was that the quantity of data required to use the model predictively was so great that once the data were gathered there would be little need for the model. In our opinion, applying Baker's model to prospecting can be less problematic for certain species and some kinds of movement. The key parameter to calculate a priori is $E_{sc}$, for which one ideally must know the expected reproductive success of an individual at multiple sites. Although this is not possible, enough data might be gathered to allow the model to be applied usefully to some species. To calculate $E_{sc}$ one must have data on the costs and benefits of prospecting, and this depends in part on
the predictability of site quality from year to year. For example, if predictability is high, then production of young at each site (whether a single nest site or a colony site) will be a good predictor of expected reproductive success and will be measurable by prospectors (e.g., see kittiwake and cavity-nesting duck examples below). Costs will vary with species and could include loss of the individual’s current breeding territory, increased risk of death while prospecting, and incorrect conclusion about which territory or site to settle. In a marked population where the observer has sufficient opportunity to observe identifiable individuals, one could get these data and assume their values did not change significantly for predictive purposes. This type of exercise, which might involve considerable averaging of data across individuals, cannot eliminate uncertainties, but all models are simplifications of the real world. It remains to be seen if a predictive model of prospecting can be developed using Baker’s (1978) model.

Another of Ketterson and Nolan’s (1983) criticisms of Baker’s model was of the threshold explicit in the model. Their concern was that there probably is no physiological reality to the concept of a cascading series of thresholds governing all nonaccidental movements (which, as noted above, Baker’s model was designed to address). In prospecting, there might be no threshold per se. The suitability of various possible breeding sites will fall along a continuum of quality, and an organism should pick the site that for it represents the best point on the continuum. The reliability of the continuum developed during prospecting depends on the quality of the data available for making decisions. Regardless of the species, however, Baker’s (1978) model is useful to ornithologists for describing and organizing a framework for investigating movement decisions. However, it is possible the settlement rules used by an individual provide it with a threshold of the minimum quality required of a breeding site, rather than the best site possible. Johnson (1989) presented a model of exploratory behavior that appears to be a simplification of Baker’s (1978). This model relates the time spent prospecting (t) to the cost (C) or benefit (B) in terms of fitness of the prospector. Further, this model assumes: the individual already has a territory; territory quality varies and high-quality territories are limited; a prospector can benefit if it finds a better territory; and the number of territories that can be investigated is finite. The more time an individual prospects, the more likely it is to encounter a superior territory. This benefit increases monotonically but becomes asymptotic. Increased search time, however, increases risk of mortality and risk that other prospectors will find and preempt the highest-quality territories. Also, the prospector could lose the territory it currently occupies (applying this model to a free-ranging individual would decrease B and increase C). As a consequence, costs rise with time at an ever increasing rate. From this model, the optimal prospecting time is when \( B - C \) is at a maximum, i.e., when \( \frac{dB}{dt} = \frac{dC}{dt} \), which occurs at some intermediate search time (essentially the same as Baker’s (1978) \( h_{max}M_e \)). Johnson (1989) makes qualitative predictions; for example, when there is spatial autocorrelation in habitat quality, prospecting over short distances should decrease cost, and prospecting time should decrease with population density. The model is not complex enough to make predictions for particular situations unless detailed cost and benefit data are available, in which case it becomes much like Baker’s (1978) model.

To our knowledge, Boulinier and Danchin (1997) have the only other model of prospecting for information regarding breeding-site selection. Their Monte Carlo simulation compares expected lifetime reproductive success between individuals settled at a randomly selected site and individuals that prospect and use data from reproductive success of conspecifics as the criterion for settling. Their aim was to determine in what conditions it may be valuable for an individual to investigate potential breeding patches at the end of the breeding season, i.e., at a time when the local reproductive success of conspecifics can be assessed readily. The model incorporates habitat patches that are good (probability of breeding successfully = 1) and bad (\( P = 0 \)). The proportion of good and bad patches is set as constant in the environment, but the individual quality of the patches varies annually depending on the level of autocorrelation of the environment. The model associates prospecting with a high cost: Individuals could not breed during the year in which they prospect. Despite this cost, the authors found prospecting is a better strategy than is random settling, provided patch quality is sufficiently predictable from one year to the next. This result clearly underlines the potential adaptive significance of prospecting and the need to look at the spatiotemporal variability of the environment. This model was designed for territorial, migratory species with a patchy distribution and long life. However, it could be adapted to fit any life-history pattern. For example, one could eliminate the assumption that a bird cannot prospect and breed in the same year.

2.2. Models of Other Forms of Vertebrate Spatial Behavior

Spatial models from many fields of research could be adapted, and would contribute, to increasing the sophistication of prospecting models. Because of space limitations, we present only two examples,
which are from the fields of metapopulation dynamics and mate selection, respectively. We do not present models from the foraging literature, although several are relevant (e.g., Anderson et al., 1997), particularly those concerning when to stay versus when to move among sites (Stephens and Krebs, 1986). Fundamentally, all spatial models are similar in positing the existence of multiple choices with differing fitness consequences and asking how the organism can optimize the time (or distance) spent searching for superior options.

A metapopulation is a group of populations, each of whose local dynamics is affected by dispersal among the various populations in the group (e.g., Wu et al., 1993). Although metapopulation models traditionally ignore the behavioral element of dispersal expressed in many species (Reed, 1999), Pulliam and Danielson (1991) present a spatial model in which the cues leading to immigration and emigration readily adapt themselves to prospecting decisions. Thus they start by modeling territory selection within a single habitat, then expand to territory selection among habitats. Both processes are expedited by prospecting; in fact, the model assumes prospecting occurs. Pulliam and Danielson (1991) expanded Fretwell and Lucas’ (1970) ideal free distribution model by not assuming individuals have perfect knowledge of the environment. An individual’s goal is to maximize its expected reproductive success \( E(RS) \). It does so by comparing quality of territories, which is measured as \( \beta_i(n) \), the mean reproductive success in territory \( i \) when there are \( n \) individuals present. This model has several interesting features relevant to prospecting. First, \( E(RS) \) varies with population size; as the best breeding territories are filled, mean RS of available sites declines. Second, the choice of breeding site improves as number of sites sampled increases; only when searches include all available territories (i.e., knowledge is perfect) does the model become ideal free. However, the tradeoff between search time and \( \beta_i(n) \) is not linear; increased searching improves \( E(RS) \) in ever decreasing increments. Therefore, there is an optimum search time, and because \( E(RS) \) declines with increasing population size, the optimum search time rises when there are more choices. More choices means more territories unoccupied (i.e., \( n \) is small). As stated, Pulliam and Danielson expanded the model by including a second habitat. The goal becomes selection of the best territory across the two habitat types, which requires comparing \( \beta_i(n) \) between the two.

In using this model for predicting prospecting decisions, the options vary with one’s goals. One could model general areas, such as breeding colonies, by simply using the single-habitat model and treating each colony as a territory. In this case, all individuals within a breeding colony would be treated as equal. Because some bird species when prospecting at a colony appear to assess overall reproductive output and to use that information as the basis for choosing among colonies (e.g., Fisher and Fisher, 1969), the single-habitat version might be adequate. Individuals of some species, however, clearly assess the quality of individual territories within a breeding area (e.g., Zicus and Hennes, 1989). If prospecting in these species is done at only a single site (which is unlikely, except during within-season movements) the single-habitat model can still be used. If prospecting is done at multiple sites, Pulliam and Danielson’s multihabitat version is appropriate. For example, if a prospecting bird is selecting a territory in one of two habitats, selection would be arbitrary when

\[
\frac{n_i}{s_i \Delta_i} = \left( \frac{n_2}{s_2 \Delta_2} \right)^{\alpha_i/\alpha_2},
\]

where \( n/s \Delta \) is the proportion of breeding sites occupied in a given habitat and \( \sigma \) is the mean reproductive success at a site.

In Pulliam and Danielson’s (1991) model, habitat quality is measured by expected reproductive success, but it could be measured by any factor that a species is known to use. The model was developed for species that select a breeding site immediately before they breed (before “summer”), when reproductive success of present occupants of the site could not be used to assess habitat quality. However, this model can be applied to prospectors that make their selection at the end of the breeding season, when some bird species do appear to prospect (see below), and indices of reproductive success (e.g., presence of juveniles) during the season just ended could be the basis for predicting habitat quality in the following year.

One problem for a prospecting bird (and for a researcher) is that reproductive output might not accurately reflect habitat quality (Watkinson and Sutherland, 1995). However, reliance on some information is usually better than random settlement (Wootton et al., 1986; Baker, 1978). In addition, data reflecting recent reproductive success could be supplemented during prospecting (regardless of its timing) by information about related matters, such as presence of competitors (Cody, 1981), prey availability (Greenwood and Harvey, 1978), or abiotic factors (Tyler and Ormerod, 1994; Oelke and Kloper, 1970). It is reasonable to believe that individuals prospecting long before they breed (e.g., their maturation is delayed) modify their decisions based on newly available data gathered immediately before settling. This behavior could be incorporated explicitly or implicitly into Pulliam and Danielson’s model.
Models of mate selection also can be adapted to the process of prospecting for breeding sites. The concept of the existence of a threshold that must be exceeded before a choice is made is explicit in Baker's (1978) prospecting model and Pulliam and Danielson's (1991) metapopulation model and is also present in many models of mate selection (e.g., Orians, 1969). In all of these processes, as well as in spatially explicit foraging decisions (Stephens and Krebs, 1986), an individual gathers information across space and uses the information to make decisions. The biggest difference between the decisions made in these cases and those made in choice of breeding site following prospecting is the time lag between gathering the information and using it, which often is much longer for breeding-site decisions. The time element, however, will not affect the relevance of any of these models except through the quality of the information, which might degrade with time.

Wiegman et al. (1996) compared two mate-selection models that have obvious parallels to prospecting for breeding sites: sequential search (optimal threshold) (Real, 1990, 1991) and best-of-$n$ (where $n$ is the number of potential mates sampled) (Janetos, 1980). Wiegman et al. tried to determine which model worked better in theory and what data need to be gathered to contrast the predictions of the models. In the best-of-$n$ rule, a female samples $n$ potential mates and returns to mate with the best male. In the sequential search model, a female initially sets a minimum threshold for expected fitness and mates with the first male she encounters that exceeds the threshold. In the former the question for the female is how many males to sample, and in the latter it is where to set the threshold. Both models base their decisions on balancing expected costs and benefits of sampling, and both have the potential for adaptation to modeling prospecting. Wiegman et al. (1996) found the sequential selection model was better (i.e., produced higher expected fitness) when there was a cost to searching and that the differences between the models was least when costs were very high or very low.

In the best-of-$n$ model, the female chooses the number of mates to sample that maximizes expected fitness $R(n)$.

$$R(n) = E(W^*_{n}) - cn,$$

where $W^*_{n}$ is the maximum fitness that results from assessing $n$ males, and $cn$ is the cost of assessing $n$ males. Once the optimum $n$ is determined, a female then samples exactly $n$ males before deciding with which to mate. $E(W^*_{n})$ increases with sample size, but so does cost. In contrast, the sequential search model predicts a female will mate with a male if that male's quality exceeds a threshold, $W > W_{min}$ (Real, 1990). Calculating $W_{min}$ is key and, as with all of the models considered herein, this occurs when the costs of continued searching outweigh the benefits of gathering additional information. Reid and Stamps (1997) provide an example of testing a threshold model for mate selection, providing costs and benefits of searching for additional mates.

In both best-of-$n$ and threshold models, increasing the cost of search decreases the expected extent of the search. However, the most interesting results with regard to prospecting are due to information's being imperfect and to variability among individuals. Individuals setting a threshold for settling, or determining how many sites to visit before settling, differ in experiences and perceptions (e.g., Klopfer and Hailman, 1965). If we assume sites are encountered sequentially and randomly (as these models assume), then by chance some birds will visit relatively more good sites than will other birds. In addition, the sample size for the experienced breeder will be greater if it incorporates information across years. Thus, it will have better information on the relationship between expected and actual reproductive success. This means individuals will differ in where they set a threshold for settling, in part owing to chance and in part owing to experience. The latter factor could be important in explaining why older birds have better reproductive success than younger birds, and it predicts that older migrants might settle earlier in the breeding season (i.e., they require less sampling to determine $W_{min}$).

It is important to remember that model development could quickly outstrip our abilities for testing. All of the models referred to require some measurement of habitat quality (or expected reproductive success) and some test of the costs of prospecting, and gathering these data can be difficult. Muller et al. (1997) provide an example of data collection and model testing in House Wrens (Troglodytes aedon), where conspecifics are the source of information on habitat quality. Experimental manipulations for testing some aspects of prospecting behavior are possible (cf. Nolan and Ketterson, 1991; Ketterson and Nolan, 1990), but manipulating organisms that use large spatial scales is more difficult than many manipulations (e.g., clutch size) done in breeding experiments. So while model development is important, it also is crucial that it be tied to testable hypotheses.
3. LITERATURE REVIEW: OBSERVED PROSPECTING PATTERNS

3.1. Methods

We reviewed the literature using the following methods: (1) We did computerized searches in Biological Abstracts and Uncover under words associated with prospecting behavior. The behavior by which an animal gathers information on potential future breeding sites has been referred to in the literature as pioneering (Hochbaum, 1946), exploratory behavior or exploratory ranging (Baker, 1978; Nolan, 1978), prospecting (e.g., Boulinier et al., 1996; Imber and Lovegrove, 1982), ranging (Grinnell, 1900; Baker et al., 1982), reconnaissance (Reed and Oring, 1992), and habitat sampling (Badyaev et al., 1996). We also searched the terms “float,” “molt migration,” and “movement.” (2) We surveyed the literature itself for mention of behavior that could be interpreted as prospecting. Journals surveyed were Animal Behaviour, Auk, Avian Ecology, Behavioral Ecology, Condor, Ibis, Journal of Field Ornithology, and Wilson Bulletin. We also searched Birds of the Western Palearctic (Cramp and Simmons, 1977, 1980, 1983; Cramp, 1986, 1988, 1992; Cramp and Perrins, 1993). (3) When we found papers describing what we interpreted as prospecting, we examined their Literature Cited sections. (4) We did ad hoc reviews of potentially related symposia and books and of potentially related migration literature and also drew upon an accumulation of references on movement that had come to our attention over the years.

Table I lists 103 species for which we found published evidence that we interpret as prospecting. This information was presented largely incidentally to some other, principal subject of the various papers. As stated earlier, prospecting per se has been studied infrequently, which means Table I is not an exhaustive list of the species that engage in the behavior and also that we cannot compare the prevalence of prospecting across different groups.

3.2. Behavior Interpreted as Prospecting

The behavior that most clearly constitutes prospecting is visiting nests built by other individuals. Visiting takes several forms, including looking into nesting cavities at the end of the breeding season, examining the contents of in-use nest cavities while perched at the rim, and squatting in active nests containing eggs or chicks. These behaviors were performed most often by individuals whose nests had failed recently, by individuals that had not yet bred or had bred
<table>
<thead>
<tr>
<th>Species</th>
<th>Age (yr) at first breeding</th>
<th>Solitary or colonial nester</th>
<th>Nest Location</th>
<th>Nest Visibility</th>
<th>Status of prospectors</th>
<th>Behavior of prospectors</th>
<th>Timing</th>
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<tbody>
<tr>
<td>Snow Petrel, <em>Pagodroma nivea</em></td>
<td>5–14</td>
<td>C/S</td>
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<td>L/E</td>
<td>Chastel et al., 1993</td>
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<td>Blue Petrel, <em>Halobaena caerulea</em></td>
<td>C</td>
<td>F</td>
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<td>Pr</td>
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<td>Harper, 1976; Richdale, 1965a</td>
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<td>Fairy Prion, <em>Pachyptila turtur</em></td>
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<td>C</td>
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<td>Richdale, 1965a; O. Chastel,</td>
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<td>Slender-billed Prion, <em>P. belcheri</em></td>
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<td>personal communication (to E.D.)</td>
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<td>1992; Jousain et al., 1977, 1980a,</td>
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<td>C</td>
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<td>and Curry, 1984; Serventy, 1967</td>
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<td>1973; Harris, 1965</td>
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<td>C</td>
<td>V/F</td>
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<td>Im</td>
<td>IN</td>
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<td>Richdale, 1964, 1965b</td>
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<td>V/F</td>
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<td>Im, NB</td>
<td>SQ, Pr</td>
<td>L/E</td>
<td>Harris, 1969; Allan, 1962</td>
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Palestine Sunbird, Nectarina aesa  
Field Sparrow, Spizella pusilla  
White-crowned Sparrow, Zonotrichia leucophrys  
Dark-eyed Junco, Junco hyemalis  
Prairie Warbler, Dendroica discolor  
Orange-crowned Warbler, Varnivora celata  
Red-winged Blackbird, Agelaius phoeniceus

*P: nest on flat surfaces (e.g., ground, reed beds, slopes); V: nest on vertical surfaces (e.g., tree, building, rock or sand cliffs).  
*V: nest contents readily visible to prospectors (nest open, contents uncovered); H: nest contents hidden to prospectors (nest closed, e.g., domed or in cavity, burrow, hole in tree, building; dense vegetation around nest).  
P: prospecting by adults capable of breeding but not breeding in current season (includes floaters); PB: prospecting by breeders in current season, usually after breeding attempt has failed.  
*Pr: prospecting during breeding season in habitat suitable as breeding site but does not breed there, in some cases returns later to breed; IN: in addition to appearing, nonbreeder enters territory of conspecific; VC: enters breeding territory of conspecific and inspects nest (usually a cavity; behavior usually at or after end of breeding season); CC: enters breeding territory of conspecific, lands on nest-cavity entrance and inspects contents; SQ: enters breeding territory of conspecific, squats on nest containing eggs or nestlings; TB: enters breeding territory of conspecific, fights with owner or with another conspecific; US: enters breeding territory of conspecific and uses its nest; Adp: enters breeding territory of conspecific that has disappeared, adopts its eggs or nestlings; HE: acts as helper; ISA: visits breeding site of heterospecific.  
*L: most prospecting occurs toward end of breeding period; E: most prospecting occurs early in breeding season, before settlement has been completed; E-L: prospecting may occur throughout breeding season.
successfully in the current year, or by individuals whose breeding experiences were unknown at the end of the breeding season.

When an individual bird that was not known to be a local breeder engaged in territorial behavior (e.g., fighting on a territory held by a conspecific) during the breeding season, the behavior was interpreted as prospecting as a preliminary to a breeding attempt that same season. When it occurred too late to permit a new attempt to breed, it was presumed to be assessment for the following year. Actual usurpation of a nest in use was treated as having been preceded by prospecting in the current year.

Some behaviors were categorized as prospecting even though searching for future breeding sites might not have been a primary goal. As stated, we reasoned that information could be gathered and used in selecting future territory locations. These behaviors included acting as a supernumerary adult (helper) on a territory occupied by a breeding pair, adopting dependent young whose parents apparently had disappeared, and intruding (by an individual not a local resident) on an occupied territory. As described, a bird reported to occupy a vacant site temporarily also was assumed to be gathering information on its suitability for breeding and was considered a prospector.

In addition to cases in which birds landed at nests built by other individuals, we treated settlement in colonies occupied by conspecifics or heterospecifics as being the result of prospecting. That is, if individuals appeared to have been attracted by the presence of others, we assumed they had experienced sites not occupied by other birds and that they preferred to breed in the presence of other birds.

Veen (1977) reviewed evidence of interspecific attraction in Sandwich (Sterna sandvicensis) and Common terns (S. hirundo) and Common Black-headed Gulls (Larus ridibundus). Using decoy Sandwich Terns, he showed that one could create a new cluster of Sandwich Terns in the vicinity of a colony. This cluster also attracted breeding pairs of Black-headed Gulls that established their nests among the dummy and the live terns.

3.3. Summary of Literature Review

Although the data in Table I are not exhaustive and we cannot reliably compare prospecting across groups, certain conclusions are clear. Prospecting for breeding sites is performed by many different taxa, having a wide variety of life-history patterns. As a consequence, we argue that prospecting is widespread. Some prospectors are colonial and others solitary, some short- and other long-lived (age at first breeding varies from 1 to >13 year old). In short-lived species, prospecting sometimes appears immediately after young become independent; these individuals do not engage in behavior associated with nesting (such as squawking on nests). Yet members of long-lived species may prospect during several or many breeding seasons. Certain of these longer-lived species even appear to use information from other avian species to assess the attractiveness of breeding sites.

Table I also reveals that when prospecting occurs in a species it seems to be common in immature individuals. Adult prospectors often are, as stated, breeders whose nests have failed or individuals that have not nested in the current year.

4. INFORMATION: ACQUISITION AND USE

4.1. Types of Information

Probably the most important factor affecting the efficacy and efficiency of prospecting, and therefore whether a species will prospect, is the quality of available information, i.e., its reliability in predicting local reproductive success (cf. Stephens, 1989). The most readily available environmental information that might be useful is knowledge of a site's land-form pattern and plant community, which might indicate whether it would produce cover for nesting and food (e.g., Blue-Gray Gnatcatchers, Polioptila caerulea; Root, 1967). Similar environmental information that might be available includes such facts as numbers of nest cavities and predator density. Potentially more reliable information would be presence and numbers of breeding conspecifics, abundance of chicks, and operational sex ratio. Correlates of past use also may be informative, such as presence of last year's nests of conspecifics or even of heterospecifics (Martos and Johnson, 1996; Yahnner, 1993; Erickmann et al., 1990). [Some species use old nests of heterospecifics; among these are Solitary Sandpipers (Tringa solitaria), which breed in old passerine nests (Oiring, 1973).]

Another type of information that can be used by prospecting individuals is knowledge gained from experience, e.g., past reproductive success. This includes personal experience (Switzer, 1993; Marzluff, 1988) or that of a potential mate (Oiring et al., 1994). In some species, individuals whose reproductive attempts have failed disperse more often than do birds with successful nests (e.g., Desrochers and Magrath, 1993; Schieck and Hannon, 1989; Brooke, 1978; Nolan, 1978:343–354, ch. 37), which implies that success is a standard by which current sites
are judged (which might make Real's [1990] sequential search model effective for modeling prospecting). Potential dispersers might prospect while the current nest is still active and use the exploratory information garnered during prospecting if they disperse at a later time (e.g., Havlin, 1991; Nolan, 1978:343). As an example of behavior in reliance on vicarious experience, although the example does not involve prospecting, in many species, particularly waterfowl, young rely on their parents (i.e., accompany their parents) in selecting migration routes and winter sites (e.g., Johnson and Raveling, 1988). In addition, ducks of many species pair on the wintering ground and males then migrate with their mates, which return to their breeding sites of the preceding year (Oring and Saylor, 1992).

4.2. Conspecifics as Sources of Information

Possibly the most reliable source of information to a would-be settler is the presence and behavior of conspecifics. This has been proposed as a basis for foraging-site selection (e.g., Pöysä, 1991; Kiester and Slaskin, 1974), and the argument also applies to selection of a breeding area. Conspecifics are known to provide cues for selecting breeding sites in several taxonomic groups other than birds. These include marine invertebrates (Minchinton, 1997; Burke, 1986; Scheltema et al., 1981), beetles (Grevstad and Herzog, 1997), spiders (Samu et al., 1996), lizards (Stamps, 1987, 1988, 1991), and mammals (Weddell, 1991; Hoek, 1982, 1989). In birds, conspecific cues about habitat quality would consist not only of the visible presence of other individuals (e.g., Muller et al., 1997; Brown and Bomberger Brown, 1996; Brown et al., 1990; Shields et al., 1988) but also of their songs (Eens, 1994; Verner, 1992; Mountjoy and Lemon, 1991; Alatalo et al., 1982; Boag, 1976). Presumably more important would be evidence of reproductive success (e.g., Boulainier and Danchin, 1997; Boulainier, 1996; Reed and Oring, 1992; Danchin et al., 1991; Slagsvold and Lija- jeld, 1990; Fisher and Fisher, 1969). This is notably the case in Black-legged Kittiwakes, in which local reproductive success was found to be temporally predictable and to be associated with site fidelity and recruitment (Danchin et al., 1998).

Information based on conspecifics is never perfect, of course. Parrish (1995) suggested that some Common Murres (Uria aalge) colonies grow despite the fact that these colonies suffer predation (predation at the time of prospecting does not necessarily predict predation in subsequent years). Furthermore, and without respect to predators, the presence of conspecifics could become a liability; with increased den-

sity could come increased competition for resources. In short, the quality and uses of information are likely to be complex and to be determined by aspects of the biology of the particular species involved.

4.3. Timing of Availability of Information

The types and quality of information on the suitability of a prospective breeding site vary with time (Brewer and Harrison, 1975); for example, chicks are present during only part of the breeding season. Therefore, the timing of prospecting is expected to be affected by the data available for assessment and the probability that the prospec- tor will be able to settle if it finds a suitable site. This probably means most prospecting will occur either at the beginning of the breeding season or at its end. Early prospecting could allow prompt selection of a site for the new season and, in the case of the mate-choosing sex, choice and acquisition of a partner. Late-season prospecting would allow evaluation for settlement in the following year.

Although prospecting at the beginning of the season sometimes might permit individuals to select and settle a site immediately, Brown et al. (1990), point out that early in the season Cliff Swallows (Hirundo pyrrhonota) probably are unable to rely on colony size as a cue because the colony is not yet fully formed; its ultimate size may be unpredictable. Birds that assess correlates of previous reproduction (cues lasting from the previous season, e.g., old nests) may be unlikely to prospect at the beginning of a breeding season (Yaher, 1993; Erckmann et al., 1990). Nevertheless, Reed and Oring (1992) found that in Spotted Sandpipers (Actitis macularia) visitors to a site at the beginning of the season returned to breed there the following year. Most species show sequential settlement of sites, with the older, more experienced individuals (especially the socially dominant sex) settling first and usually choosing their sites of the previous year (e.g., Nolan, 1978:20–22, ch. 37).

Our literature review reveals that in most species prospecting occurs mainly toward the end of the breeding season (Table I), and therefore it is probably used to assess potential sites for the following year (Boulainier and Danchin, 1997; Danchin and Wagner, 1997; Boulain- lier et al., 1996; Baker, 1993; Reed and Dobson, 1993; Reed and Oring, 1992; Zicus and Hennes, 1991; Shields et al., 1988). This suggests two competing hypotheses: 1) the habitat can be assessed more accurately at the breeding season's end rather than its beginning; or 2) the costs associated with late-season assessment are lower, perhaps because extensive prospecting in the spring might result in missed breeding.
opportunities in the current year. We propose some cues collected at the end of breeding are better predictors of site quality than those available at the start of the season (Boulinier et al., 1996; Bollinger and Gavin, 1989; Burger, 1982). Reproductive success of conspecifics during the year of prospecting might be the most accurate predictor of future potential (Boulinier and Danchin, 1997; Danchin and Wagner, 1997; Beletsky and Orians, 1991; Danchin et al., 1991; Bollinger and Gavin, 1989; Shields et al., 1988), provided the environment is relatively stable from year to year (Boulinier and Danchin, 1997; Switzer, 1993).

Examples of prospecting demonstrate interspecific variation in timing and its relationship to the types of information available. Newly fledged White-crowned Sparrows (Zonotrichia leucophrys) wander extensively before migration (Morton, 1992), when available data include location of late breeders, habitat structure while deciduous plants and annuals are still green, late-season food availability, and recently used nests, among other cues. Some cues might be ambiguous, such as late-season breeding, which might characterize either a site at which multiple broods were produced or one at which early-season predation caused breeding to be late. However, the presence of breeders does provide some information, and additional cues, such as possible information on the presence of fledglings, can improve site assessment.

Reed and Oring (1992) found Spotted Sandpipers prospect during two seasonal peaks, one about a week after the peak of arrival of breeders in spring and a second about a week before a wave of departures by breeders in autumn. Prospecting at these peaks provides different information: the first relevant to the current season and the second to the following season. Subadult Black-legged Kittiwakes may prospect at all times during several breeding seasons before they select their first nesting site (Boulinier et al., 1996; Cadiou et al., 1994). Similar timing is exhibited by adults of some obligate cavity-nesting ducks, such as Common and Barrow’s goldeneyes (Bucephala clangula and B. islandica), Bufflehead (B. albeola) (Zicus and Hennes, 1989; Dow and Fredga, 1985; Edie and Gauthier, 1985) and Shelducks (Tadorna tadorna) (Patterson and Makepeace, 1979).

4.4. Sexual Selection and the Value of Information

Individuals of the two sexes often are under different sexual selective pressures; thus, the same item of information might differ in value to males and females. This could affect the likelihood or the manner of prospecting by the two sexes. The Spotted Sandpiper provides our only example of this. In this polyandrous species, lifetime reproductive success for females is dependent on the number of mates acquired, whereas males, because they can have only one successful clutch per year, are not under the same selective pressure (Oiring et al., 1991). Both sexes engaged in what Reed and Oring (1992) described as prospecting. However, prospecting females apparently responded to information on local reproductive success (i.e., their return rate in the following year was correlated with rate of reproductive success in the year of prospecting), whereas males did not (See Section 7.1.). It is therefore possible that females were prospecting and transient males were not, despite their exhibiting apparently the same behaviors. It is reasonable to believe that in other species under strong sexual selection sexual differences in prospecting might also prevail.

5. PATTERNS OF DISPERAL

Prospecting for future breeding sites follows patterns primarily related to life history and patterns of dispersal. Dispersal commonly is treated as a mechanical or diffusional flow whereby an animal leaves its natal or breeding territory and travels along some course, then settles at an appropriate site (e.g., Johnson and Gaines, 1990; Holt, 1987; Waser, 1985). Dispersal typically is presented in the literature as a matter of “the number that goes here” or “males go, females stay” (e.g., Greenwood and Harvey, 1982; Greenwood, 1980, 1983) or the like. This approach often is implied or applied in theoretical work on dispersal (e.g., Caley, 1991; Shields, 1983). In metapopulation studies, dispersal usually is framed as a problem of the proportion or number of individuals that enter the general pool of migrants among patches, or it is assumed to follow a given probability function (Hanski and Gipin, 1991, 1997). However, dispersal in birds is a behavioral as well as a population or quantitative process, even when it involves density-dependent movement to obtain resources (e.g., Gowaty, 1993; Rodgers, 1990; Howard, 1960) or to find mates (e.g., Waser, 1985). Our concept of prospecting assumes that dispersal performed by prospectors is the result of an informed choice based on data gathered in advance of decision. The proposition that animals gather information about potential breeding sites and use this information in site selection is important because it ties the behavior of dispersal to the dynamics of populations.

Since dispersal patterns exist as a continuum (cf. Baker, 1978), we
anticipate a wide variety of prospecting patterns and opportunities and consider these next. Many of the following patterns have been observed in birds, but some have been reported only in other taxa. We first present potential prospecting patterns for nonmigratory species of birds, then those possible only for migratory species. Within each classification, when appropriate, we deal first with individuals searching for a site for the first reproductive attempt of life, then with experienced breeders.

5.1. Nonmigratory Birds

The simplest form of dispersal consists of leaving the natal site and settling in the first available space (Figure 1a), a behavior referred to by Baker (1978) as "noncalculated [because no prior information is used] removal migration." (Recall Baker defines any nonaccidental movement as a migration, with no implication of a to-and-fro pattern.) By definition, individuals dispersing in this way are not engaging in prospecting. But if the pattern is modified so that dispersers travel some minimum distance before settling (Howard, 1960), prospecting then becomes a theoretical possibility. It would be realized if the individual accumulated information about its surroundings while traveling the minimum distance and selected its breeding site by comparing it with sites seen along the way (Figure 1b). An extension of this type of dispersal consists of establishing a familiar area, expanding it in successive increments, and finally selecting a breeding site within it (Figure 1c). That case differs from the preceding one only in that the prospectors, having examined sites within the familiar area, may return to breed at a location with which it became familiar at an early stage of its prospecting. This behavior has been observed in the red fox (Vulpes vulpes) (Woollard and Harris, 1990) and in Eastern Screech-Owls (Otus asio) (Belthoff et al., 1993; Belthoff and Ritchison, 1990).

We envisage three special variant forms of this last pattern of behavior; all forms are exhibited by birds. First, some species use a natal or a current breeding site as the base from which to make repeated exploratory forays into the surrounding area, where they often find a location for a breeding attempt (e.g., Havlim, 1991) (Figure 1d). Such prospecting is particularly common in cooperative breeders, in which a base site is occupied by a group of nonbreeders and breeders; supernumerary birds (nonbreeders) become familiar with surrounding breeding sites and move into them when vacancies arise (e.g., Hannon

![Figure 1](image-url)

**FIGURE 1.** Possible dispersal patterns for nonmigratory species. Circled O represents individual's origin (natal site if it has not bred previously). Other labeled circles represent breeding sites or possible breeding sites and are defined as follows: (a) Dispersing individual selects first available breeding site (B) after departing from its natal site. There is no prospecting; line is not straight because individuals probably do not travel in a straight line. (b) Individual travels minimum distance before settling; may gather information en route and use it to establish criteria for selecting a breeding site. Settles in first adequate site after traveling the minimum distance. (c) Individual expands home range outward from natal area, gathering information about increasingly large familiar area. This prospecting might occur in waves; thus multiple dashed circles or ellipses. Eventually selection of breeding site within familiar area. (d) Cooperative breeder pattern: Individual moves frequently to and from a home base and monitors adjacent breeding territories (T) occupied by other breeding individuals or groups; finally takes over first adjacent territory that becomes available. (e) Floater pattern: Similar to the cooperative breeder pattern except floater does not have discrete localized base. Pattern could also be exhibited by migrants that return to breeding range and become floaters. (f) Colonial breeder pattern: Individual monitors multiple breeding colonies (C), eventually selects one as breeding site when it becomes available. Pattern could also be exhibited by migrants that return to breeding range.
et al., 1985; Woolfenden and Fitzpatrick, 1984; Ligon and Ligon, 1978; Gaston, 1976). A second variant is sometimes presented by floaters, i.e., nonterritorial individuals (usually young) that manage to exist in populations of territory holders but move about without establishing territories of their own. A floater monitors breeder-occupied territories, waiting for a site to become vacant; it then takes possession (e.g., Smith and Arcese, 1989; Smith, 1978) (Figure 1e). A third variant of dispersal following prospecting is usually done by the young. It consists of living in a breeding colony (or moving about among colonies) and monitoring multiple sites then taking over a site when that becomes possible (Figure 1f). This, the most studied prospecting pattern, is common in colonially nesting seabirds (e.g., Halley et al., 1995; Danchin et al., 1991; Monnat et al., 1990; Danchin, 1988b; Pierotti, 1987; Fisher and Fisher, 1969).

5.2. Migratory Birds

Migratory birds must leave their natal or breeding area for some months before returning to breed. Several of their theoretically possible modes of dispersal do not involve prospecting. Programmed philopatry of a first-time breeder would cause it to return to its precise natal site (Figure 2a), with no gathering of information about other locations. Such a bird would, in effect, possess an internal selection standard that specifies only the natal site as acceptable. Natal philopatry could be replaced in this sequence by programmed dispersal to, and selection of, the first site encountered after return to the breeding range or some portion of it, also with no advance gathering of information except what was observed before the return (Figure 2b). Return from the wintering ground to a site never previously explored also could be the result of pairing on the wintering ground and following the mate to the breeding site that the mate selects (Figure 2c), as is observed in many species of waterfowl (Oring and Saylor, 1992). All these patterns for first-time breeders also could be found in experienced breeders.

Patterns of dispersal that involve prospecting by migratory birds, both young of the year and adults, can be divided according to whether the behavior occurs before or during post-breeding migration or after return to the breeding ground at the beginning of the next season. A function of movement in the area around the natal or breeding site prior to migrating (Figure 2d) may be that the individual gathers information and develops a familiar area to which to return the following year (e.g., Baker, 1993; Morton, 1992; Reed and Oring, 1992; Morton et al.,...

Young of some species move northward after fledging and before migrating (e.g., herons and egrets [Ardeidae]: Erwin et al., 1996; Byrd, 1978; Siegfried, 1970; Coffey, 1943; Townsend, 1931; Bald Eagles, Haliaeetus leucocephalus: Hunt et al., 1992; White-crowned Pigeons, Columba leucophaula: Strong and Bancroft, 1994). Although the primary function of these movements might be to gain access to rich foraging sites (e.g., Shealer and Kress, 1994), the wandering might also be used to gather information about future breeding sites (Figure 2d). This possibility was proposed by Baker (1978, 1993), who made no distinction between northward and southward premigratory movements from the natal or breeding site. The northerly movement might serve to develop a large target to identify during return migration (e.g., Green and Hiron, 1991; Kelly and de Capita, 1982). (Note that normal southward migration may serve to enlarge the target in that direction.)

Finally, prospecting may be postponed until the individual returns from migration at the beginning of the next breeding season. (Figure 2e).

6. PROSPECTING BEFORE FIRST BREEDING

In many migratory and nonmigratory bird species, juveniles move away from the natal area when they become independent (e.g., Lindsey et al., 1991; Belthoff and Ritchison, 1990; Bauer, 1987; Catchpole, 1972). Common explanations for this departure include: the young are expelled by their parents (e.g., Strickland, 1991); they seek a molting area (e.g., Morton, 1991; Goethe, 1961; Coombes, 1950) or a winter home range (e.g., Tyler et al., 1990); or food availability has declined locally (e.g., Kenward et al., 1993; Frazer et al., 1990). An alternative explanation, which does not include the others, is that movement from the natal site permits young birds to gather information about possible future breeding sites, i.e., that young birds prospect.

Juveniles probably would benefit more than adults from prospecting: The only spatial information within their experience concerns the natal site and that it constituted suitable breeding habitat. In species in which plumage maturation is delayed, information gathering would be facilitated because young males could explore with relatively little harassment from territorial males (Rowher, Fretwell, and Niles, 1980).

Below we review selected examples of prospecting by juveniles and subadults. Other examples are in Table I.

6.1. Nonmigratory, Noncolonial Species

Species that do not migrate must find suitable quarters for the winter and in doing so might select a breeding site for the following spring. Eurasian Nuthatches (Sitta europaea) provide an excellent example of this behavior in a noncolonial species. After independence, juvenile nuthatches either form pairs and become territorial in unoccupied habitat, or they remain unpaired and nonterritorial (Enoksson, 1990; Matthyssen, 1987, 1989; Matthyssen and Dhandt, 1983). A juvenile prospecting before and during winter for a spring territory can use (and nuthatches do use) more than one method. It can gather information on suitable locations and the distribution of territorial individuals and (1) occupy a site that will be adequate for breeding in the coming season, or (2) occupy an inadequate site and shift when and if a superior site becomes available, or (3) without settling, monitor occupied sites and take possession when one becomes available (the Underworld Strategy, sensu Smith, 1978; see Section 7.3.). These patterns also are observed in Black-capped Chickadees (Parus atricapillus) (Weise and Meyer, 1979) and Great Tits (P. major) (Dhandt, 1979).

6.1.1. Cooperative Breeders

Cooperative breeders comprise a subset of nonmigratory, noncolonial species. They often hold year-round territories. They are characterized by the presence of supernumerary, nonbreeding adults, usually related to the breeders. These assist the breeders in some or all activities associated with reproduction, including territory defense and parental care (e.g., various papers in Stacey and Koenig, 1990). Nonbreeding adults can use the group territory as a base from which they keep the surrounding area under surveillance and gather information on potential breeding sites (Woollenden and Fitzpatrick, 1984; Hannon et al., 1985; Ligon and Ligon, 1978; Gaston, 1976). An experimental demonstration was done using Red-cockaded Woodpeckers (Picoides borealis), an endangered species whose distribution is thought to be habitat-limited by the availability of suitable breeding cavities (Jackson, 1994). These birds leave their base sites and occupy potential breeding sites when they become available (e.g., Jackson, 1990; Doerr et al., 1989; Walters et al., 1988). In the experiment, artificial cavities were created in unoccupied areas surrounding territories, thus
converting them into suitable nesting locations. These were rapidly occupied, largely by supernumerary birds from nearby territories but also by experienced breeders (Walters et al., 1992a, 1992b; Copeyn et al., 1991). The speed with which these new occupants acted indicates they regularly prospected in the areas surrounding their base sites.

6.2. Migratory, Noncolonial Species

This is the group that one might think a priori would be least likely to benefit from prospecting, especially species that are habitat generalists. Nevertheless, in many species of this group independent young of the year visit areas considerable distances from their nest sites. Marked juveniles have been captured, sometimes at multiple locations, up to 5 km from their nest, and unmarked individuals are found to have entered areas in which all locally-hatched young had been marked (e.g., Baker, 1993; Ferrer, 1993; Lindsey et al., 1991; Schwabl et al., 1991; Grahn, 1990; Gonzalez et al., 1989; Fleischer et al., 1984; Berndt and Winkel, 1979; van Balen, 1979). Morton (1992; see also Morton et al., 1991; Baker et al., 1982) hypothesized White-crowned Sparrow fledglings typically disperse and select potential breeding areas before migration. Adams and Brewer (1981) proposed the same for Field Sparrows (Spizella pusilla). In an intriguing experiment designed to study imprinting, Löhrl (1959) found nestling Collared Flycatchers (Ficedula albicollis) that were displaced from their natal areas at least two weeks before completing their postjuvenile molt returned to the site of displacement. Those displaced after molting did not return. Interestingly, birds had to be allowed to fly freely in the area to which they were displaced; i.e., those kept captive at the displacement site did not return. Recent evidence showed Collared Flycatchers that dispersed relatively short distances from the natal site have higher reproductive success than those that dispersed longer distances, and this advantage might be attributable to greater knowledge of the breeding area by the short-distance dispersers (Pärt, 1990). It is unknown whether the results Löhrl observed were due to imprinting or to developing an area of familiarity through exploration. However, similar experiments by Nolan and Ketterson (1991) with juvenile Dark-eyed Juncos (Junco hyemalis) on their wintering grounds produced results favoring the latter argument as the basis for return to the winter site by young of that species. These results are exciting and suggest that some questions regarding prospecting could be addressed through field experiments.

6.3. Migratory, Colonial Species

Prospecting appears to be widespread among colonially nesting seabirds (Danchin et al., 1991; Lack, 1966). It has often been observed that subadults of colonially nesting species move from one breeding colony to another and their subsequent settlement is nonrandom, i.e., certain colonies are preferred. Atlantic Puffins (Fratercula arctica): Harris, 1983; Kress, 1978), Western Gulls (Larus occidentalis: Kress and Nettleship, 1968; Spear et al., 1990), Herring Gulls (L. argentatus: Pierotti, 1987), and Common Murres (Harley et al., 1995) visit potential breeding sites as subadults. Movement of individually marked prospectors and colonization of new habitats indicate birds return to sites they have visited. In an early study, Fisher and Fisher (1969) found subadult Laysan Albatrosses (Diomedea immutabilis) made multiple visits to breeding colonies and settled preferentially where albatross reproductive output was high in earlier years. The most extensive study on prospecting to date, however, is on Black-legged Kittiwakes, as described in the next section.

6.3.1. Black-legged Kittiwake

The Black-legged Kittiwake is a long-lived seabird that breeds on vertical cliffs in colonies of tens to hundreds of thousands of pairs. Like most seabirds, it is monogamous and shows high natal philopatry and breeding-site fidelity. The Black-legged Kittiwake has been studied in detail by Coulson and his collaborators in North Shields, England (Coulson and Thomas, 1985). In this colony, the average age at first breeding was four years. Observation of the pattern of the birds’ presence (attendance) and capture of prebreeders of known age at the colony allowed the determination of individual characteristics (age, body condition, date of arrival) in relation to the processes of recruitment to the local breeding population (Porter, 1988, 1990; Porter and Coulson, 1987). There was strong individual variability in age at first
appearance at the colony and also in age at first reproduction (2–8 yr). Most individuals were recorded prospecting in the year preceding their joining the colony as breeders, but some were recorded for several years before they bred.

In Cap Sizun, Britany, France, a detailed, long-term demographic and behavioral study of kitiwakes elucidated the spatial and temporal aspects of the processes of recruitment, including the role of prospecting (Cadiou, 1993; Danchin and Monnat, 1992; Danchin, 1987a, 1987b, 1988a, 1988b; Danchin et al., in press). This small breeding population on the southern edge of the species’ range consists of approximately one thousand pairs spread among five colonies. The investigators arbitrarily divided each colony into a series of adjacent portions (subcolonies) of breeding cliffs. They regularly recorded all breeding attempts, attendance, and behavior of color-banded birds and mapped all breeding sites using photographs. These methods allowed them to record the exact locations of all identified individuals. They defined prospecting birds as individuals present at subcolonies where they were not breeding during the current season. They recorded breeding dispersal within each colony and among colonies and related their detailed investigations of behavior of prospecting birds to the birds’ ages and to their recruitment in later years (Cadiou et al., 1994; Cadiou, 1993; Danchin et al., 1991; Monnat et al., 1990; Danchin et al., in press).

Reproductive success was spatially and temporally variable among subcolonies owing to various local environmental factors that acted at a fine scale (e.g., predation, ectoparasites), but success was temporally autocorrelated (i.e., local success was positively correlated between successive years, Boulinier and Lernel, 1997; Danchin et al., in press). This implies that a prospecting kitiwake’s reliance on reproductive success at a subcolony in a given year should be an effective strategy for breeding-site selection to predict the expected success of its breeders in the next year (Boulinier and Danchin, 1997). Furthermore, there was strong evidence that prospecting behavior in the years prior to local recruitment was used by kitiwakes to assess potential breeding sites (Boulinier et al., 1996; Cadiou et al., 1994; Cadiou, 1993; Danchin et al., 1991; Monnat et al., 1990). Birds usually were observed as prospectors in the colony or subcolony in which they eventually settled (Table II). Among those prospectors that were the most likely to become breeders the next year (those that were recorded squatting on nests with chicks; see below), there was a relationship between the probability of settlement and the amount of time they attended the colony in the year prior to recruitment (Cadiou et al., 1994; Cadiou, 1993; Monnat et al., 1990). At a local scale, there was significant natal dispersal (only 14.5% of the birds recruited did so on their natal subcolony, and none on their natal site; n = 807, Boulinier et al., 1997), and thus prospecting could be related to local dispersal and recruitment.

Most prospecting kitiwakes were subadults (Cadiou et al., 1994; Cadiou, 1993; Monnat et al., 1990; Danchin, 1988b; Danchin et al., 1987b), but adult nonbreeders and failed breeders also prospected (Cadiou and Monnat, 1996; Cadiou et al., 1994; Danchin et al., 1991; Monnat et al., 1990; Porter, 1990; Danchin, 1988b; Danchin et al., 1987b; ). Even though active nests are the most difficult for prospectors to attend owing to aggressive behavior toward them by the nests’ owners, prospectors were strongly attracted to nests with chicks, on which they squatted as soon as both breeding adults were simultaneously away foraging (Cadiou and Monnat, 1996; Cadiou et al., 1994; Cadiou, 1993; Monnat et al., 1990; Danchin 1988b; Danchin et al., 1987, 1991). Squatters visited 80% of the nests with chicks. Moreover, despite noncontinuous observation at the colonies, squatters were observed on 50% of these nests within three days of the

<table>
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<th>Behavior in 1991</th>
<th>Present, no squattting</th>
<th>Squatting, not on main cliff</th>
<th>Squatting on empty* nest, main cliff</th>
<th>Squatting on nest with chicks, main cliff</th>
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<td>Seen alive (N = 70)</td>
<td>14</td>
<td>13</td>
<td>26</td>
<td>17</td>
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<td>% of 1990</td>
<td>7</td>
<td>13</td>
<td>31</td>
<td>59</td>
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| *Colony consisted of cliffs; for observation these were divided arbitrarily into segments or subcolonies. Table refers to the most-observed subcolony as "main cliff."
| *Squatting refers to prospect’s visiting nest while owners are away and sitting on or over nest. Most squatters observed on >1 nest or on same nest more than once.
| *Nests containing no chicks, including those from which chicks fledged, are treated as empty.
first simultaneous absence of both breeders (Cadiou and Monnat, 1996). Attendance by prospectors was greater at subcolonies with high reproductive success than at subcolonies with many breeding failures (Cadiou, 1993). Prospecting peaked in the middle of the chick-rearing period; this is the time when the relative quality of each cliff can be assessed most reliably if current reproductive success is the primary indicator of future quality (Boulinier et al., 1996). Observations of prospecting in other populations of Black-legged Kittiwakes in Great Britain, northern Norway, and Newfoundland (Hodges, 1969; E. Danchin and T. Boulinier, personal observation) suggest these patterns are typical of this species over its whole range.

Thus, prospecting by Black-legged Kittiwakes appears to be an active process of sampling of potential breeding sites and probably of assessing local reproductive success (Boulinier et al., 1996; Cadiou et al., 1994; Cadiou, 1993). Similar behavior is seen in several other long-lived colonial birds, which provide ideal subjects for prospecting and recruitment studies because they breed in discrete units and take several years to select a site. These species (Table I) need to be studied in greater detail (Danchin et al., 1991; Danchin and Nelson, 1991).

7. PROSPECTING BY EXPERIENCED BREEDERS

Experienced breeders also benefit from prospecting. Individuals are well known to use personal breeding experience for decisions related to breeding-site fidelity (Switzer, 1993). For example, unsuccessful breeders of some species are more likely to disperse, both in the current season and in the following year, than are successful breeders (e.g., Desrochers and Magrath, 1993; Reed and Oring, 1993; Beletsky and Orans, 1991; Bensch and Hasselquist, 1991; Schieck and Hannon, 1989; Thompson and Hale, 1989; Nolan, 1978: ch. 30, 350–354; Brooke, 1978; von Haartman, 1949). In such species, breeding birds whose nests are still active are likely to benefit from information on the quality of local potential breeding sites, because they may later disperse to such sites if current reproductive attempts fail. In the Black-legged Kittiwake, unsuccessful breeders and mature nonbreeders engage in prospecting (Cadiou et al., 1994; Danchin, 1988b). Adult male Pied Flycatchers (Ficedula hypoleuca) sometimes disperse short distances within a breeding season, moving to higher-quality nest boxes as they become available (quality is defined by the frequency of use of the box by conspecifics in previous years; Montalvo and Potti, 1992). Montalvo and Potti (1992) hypothesized these movements are based on knowledge of the local area. If so, it must be gained by prospecting. Prospecting would be especially beneficial when breeders must depend on an ephemeral local food supply. Boreal Owls (Aegolius funereus) become nomadic when local food supplies decline, and they settle in areas where food is available (Löfgrén et al., 1986). This has been observed in other species (e.g., Furness, 1987). Below, we present examples of prospecting for breeding sites by adults, and we also examine the case of floaters.

7.1. Spotted Sandpiper

In Spotted Sandpipers sex roles are reversed. Females are polyandrous and establish breeding territories, and males hold territories within them (Oring et al., 1994, 1997; Oring and Lank, 1986; Oring et al., 1983; Maxson and Oring, 1980). When a female has laid a clutch sired by one male, she sometimes allows her territory to be subdivided between that male and others and at times encourages the subdividing process (Oring et al., 1983; Oring, 1982, 1986). Females solicit extra-pair copulations from males, and such copulations aid in securing these males as future mates (Colwell and Oring, 1989), although extra-pair copulations do not appear to result in fertilization (Oring et al., 1992, 1994). Females have from one to four mates per year. The percentage of polyandrous females varies annually between 20–100% (Oring et al., 1983, 1991; Oring and Knudson, 1972). When a female has only a single mate, she often helps incubate and brood, but her contribution in such cases does not appear to affect reproductive success (Oring et al., 1991). Spotted Sandpipers breed when one year old. Older females have higher mating success (Oring et al., 1991, as do more experienced females (Oring and Lank, 1986; Oring et al., 1983, 1991). Not surprisingly, mate availability limits annual female reproductive success (Lank et al., 1985).

Like some other shorebirds (Harrington et al., 1989; Myers et al., 1987; Källs and Byrkjedal, 1984; Holland et al., 1982), Spotted Sandpipers engage in movements beyond the limits of their breeding home range. Reed and Oring (1992) banded transient birds (those visiting their study area for periods of 1–4 days), and found peak numbers of transients present one week before most of the breeders on their study area began their southward autumn migration. Another period of frequent appearance on the study area by individuals that then disappeared occurred at the beginning of the breeding season, about one week after the peak of arrival by local breeders. Many individually
banded transient birds returned the subsequent year to the site where they had been banded: 14% (8/58) of the males returned and five bred, as compared to 42% (23/42) of the females, of which 16 bred. The number of females returning the year after they had been banded as transients was positively associated with the proportion of males in the absolute sex ratio of study-area residents during the week in which the transient females had been banded. The return rate of transient females to breed was significantly associated with the number of eggs laid at a particular site during the year in which the bird made its transient visit to that site. Reed and Oring (1992) concluded that transients prospected for breeding sites to be used the following year and information gathered by transients was more important to females than to males (see Section 4.4.)

It is possible that prospecting was not the primary function of late-season transient visits. Birds may have been searching for rich premigration food resources (Schneider and Harrington, 1981; Dare, 1977; Branson and Minton, 1976; Evans and Smith, 1975; McNeil and Cadieux, 1972) after prey declined on the transients’ breeding sites. Food on the study area where the transient Spotted Sandpipers were banded tended to be abundant well after the departure of the local breeders (Ozinga and Lank, 1986; Lank et al., 1985). Regardless, searching for food and prospecting for breeding sites are not mutually exclusive activities.

7.2. Cavity-Nesting Ducks

There is an interesting series of studies on prospecting for nest sites by obligate cavity-nesting ducks: Common and Barrow’s Goldeneye Buffleheads (Eadie and Gauthier, 1985; Grenquist, 1963), and Shelducks (Patterson and Makepeace, 1979; Young, 1970; Hori, 1964). Prospecting is done primarily by females, including single individuals and groups of birds, both adult and juvenile, and particularly by breeders whose nests have failed. When cavities are limited or when there is high variability in the quality of cavities (i.e., in reproductive success of occupants), prospecting would have obvious benefits.

In Shelducks, a prospecting individual attracts others by its behavior, and prospecting groups form; these groups are larger when populations are larger. Prospecting interferes with the activities of the cavity owners, and interference in nest building success increases with population size, possibly leading to density-dependent population regulation (Patterson and Makepeace, 1979). The benefit (if any) of a prospector’s participation in a group is unknown, but it might be to increase the opportunity to gather information about the location of nests, which are cryptic. It has been suggested that group participation reduces neophobia (fear of novel objects or situations) and thus increases the likelihood an individual will explore new sites (e.g., Coleman and Meilgren, 1994).

In the best-studied species, the Common Goldeneye, non-nesting yearling females, females whose nests have failed, and also females attending broods investigate occupied nest cavities during the breeding season and monitor their success in producing young (Zicus and Hennes, 1989). Unlike the case of Shelducks, prospecting does not appear to affect reproductive success of cavity owners (Eadie and Gauthier, 1985). Cavities in which young were produced are preferentially used the following year by birds engaged in prospecting (Zicus and Hennes, 1989; Dow and Fredga, 1988).

Prospecting behavior also has been recorded for Tree Swallows (Tachycineta bicolor) (Lombardo, 1987), another obligate cavity-nester.

7.3. Floaters

Floaters are nonbreeding birds awaiting the opportunity to breed (Brown, 1969). Floaters have been recorded in many species (e.g., Song Sparrows, Melospiza melodia, Smith and Arcese, 1989; Winter Wrens, Troglodytes troglodytes, Wesogowski, 1981; Purple Martins, Progne subis, Stutchbury, 1991; and Blue Grouse, Dendragapus obscurus, Zwickel, 1980). A floater may engage in continuous wandering until it encounters a potential breeding site, or it may restrict its movements to a small area containing a limited number of already occupied sites. The latter pattern is more frequently observed, with floaters monitoring as many as ten territories (Song Sparrows, Arcese, 1987, 1989; Black-capped Chickadees, Smith, 1984; Rufous-collared Sparrows, Zonotrichia capensis, Smith, 1978). Red-winged Blackbirds (Agelaius phoeniceus) are a well-studied example in which floaters range much more widely, encountering a large number of territories (Beletsky, 1992; Shuttler and Weatherhead, 1991, 1992). Experimental removal of territory holders caused floaters to restrict their wandering and to concentrate their activities in the areas from which territory holders had been removed (Shuttler and Weatherhead, 1991).

The presence of floaters can affect mating patterns of territory holders. Arcese (1989) found male Song Sparrows, which typically are monogamous, sometimes became bigamous when female floaters settled on territories where the resident female was already occupied with
8. PROPOSED MECHANISMS FOR INTEGRATING AND USING INFORMATION

No research has focused specifically on how birds gather, store, map, and recall information gathered during prospecting for breeding sites. To obtain such data is a daunting task, especially when eight months or more can pass between the time of prospecting and the time when the information is used (e.g., Reed and Oring, 1992). However, birds engage in behaviors that appear to pose neurological challenges analogous to those involved in prospecting. These include discovery of host nests by brood parasites and recovery of food by caching species. We view these primarily as problems of information storage and memory of point locations. A somewhat different task for a prospecting bird is that of finding its way back over long distances to such locations, and here the large body of work on orientation and navigation become relevant. Excellent research in both information storage and orientation may throw light on prospecting. Reviewing that literature is beyond the scope of this paper, but we present selected important findings that may be relevant to our subject.

8.1. Nest Finding by Cowbirds

Spatial information is processed in the hippocampal portion of the brain (Smulders et al., 1995; Sherry and Vaccarino, 1989). Cowbirds of the genus Molothrus make an ideal species complex for studying how interspecific differences in requirements for spatial memory are reflected in the structure of the hippocampus.

Cowbird species differ in mode of reproduction. Some are brood parasites, and others are not. Brood parasites must find nests of hosts and return to them at the appropriate time to lay their eggs, a problem similar to that faced by prospecting birds, although only short-term memory is required of parasitizing cowbirds. Among the parasitic cowbirds, in some species both sexes search for nests while in others only females search. Screaming Cowbirds (M. rufoaxillaris) and Shiny Cowbirds (M. bonariensis), brood parasites, have a larger hippocampus than does the nonparasitic Bay-winged Cowbird (M. badius) (Reboreda et al., 1996). In Brown-headed Cowbirds (M. ater) and Shiny Cowbirds only females search; females have a larger hippocampus than do males (Reboreda et al., 1996; Sherry et al., 1993). In Screaming Cowbirds, in which both sexes search, and in Bay-winged Cowbirds, in which neither sex searches (Reboreda et al., 1996), there is no sexual difference in hippocampus size.

Prospecting also requires spatial memory. Based on the cowbird research and examples referred to below, we conclude that prospecting should involve the hippocampus. It is reasonable to hypothesize that prospecting species would have relatively large hippocampal development, but we note an enlargement, if found, might also be associated with other requirements for spatial memory (see next subsections).

8.2. Food Caching and Recovery

Possibly the greatest amount of work on birds' gathering and recalling information in decision making comes from studies of food caching. Caching food for future use has been reviewed extensively by Vander Wall (1990) and by Källander and Smith (1990). What follows is summarized from Vander Wall (1990) except where otherwise noted.

Food caching is common in birds and other animals and is of interest with respect to avian prospecting because both activities may use spatial memory after long periods have elapsed. Arguably the most extreme example of caching is provided by Clark's Nutcrackers (Nucifraga columbiana): a single individual may store 100,000 pine seeds in caches of one to 18 seeds, all evidently to be accessible at a future time, which can be nine months later (Balda and Kamil, 1992). Nutcrackers often cover recent caches, presumably to conceal them from other nutcrackers, and eventually weather can hide a site. This could increase the difficulty of recovery by the caching bird.

Relocation of caches might (1) rely on cues inherent in the cache site either natural or created during preparation of the cache, (2) use random searching, (3) use systematic searching in areas suitable for caches, (4) be based on memory of position of the cache with reference to nearby visual cues, or (5) rely on some combination of the above. For many species, the mechanism is not known, and among others it varies. Field observations and laboratory experiments with Clark's Nut-
crackers apparently have eliminated the first three potential mechanisms and supported the fourth. Evidence supports the same conclusion for caching Marsh Tits (Parus palustris) and Black-capped Chickadees (e.g., other references in Vander Wall, 1990; Sherry, 1984; Sherry et al., 1981).

Recovery time varies among caching species, from a few hours or days (e.g., Brodin, 1994; Hitchcock and Sherry, 1990) to as much as nine months. The problem of storing and integrating information over time is exacerbated when the amount of information required for recovery of the cache increases (e.g., Dukas and Real, 1993a, 1993b). Vander Wall (1982) found that large, conspicuous objects, such as trees and rocks, serve as visual cues for triangulating cache locations; smaller objects are less important. Birds appear to use distances rather than angles in this process. Given that some species use this kind of memory for relocating sites, it is reasonable to hypothesize prospectors remember potential breeding sites in the same way, even though often for much longer periods and over larger areas.

The bird species that cache have a relatively larger hippocampus than do species that do not cache (Clayton, 1995). Experimental data on individuals within a species that were allowed to store food revealed they had a larger hippocampus than did those not given this opportunity (Clayton and Krebs, 1994; Krebs et al., 1989; Sherry et al., 1989). However, this intraspecific difference arises during development of young and cannot be induced in adults (Cristol, 1996). Therefore it may be questionable that prospecting by free-living adults affects brain structure or volume.

8.3. Navigation and Orientation

Research on animal orientation and navigation has focused largely on two very different spatial scales: short movements within a territory, home range, or laboratory set-up, and long movements usually made during migration (but see the Journal of Experimental Biology, 1996: 199(1), which deals with animal navigation over intermediate as well as short and long distances). Studies of small-scale movements are perhaps epitomized by experiments on rats in mazes (e.g., Gallistel, 1990; Leonard and McNaughton, 1990), and studies of large-scale movements by studies of migratory birds. Recent reviews of the very large body of literature on avian orientation and navigation include those of Berthold (1991, 1993), Able (1995), and Witschko and Witschko (1995).

Both large and small scale research on orientation has shown animals use a multitude of cues, the utility and availability of which may vary according to the nature of the movement (Able, 1995; Jander, 1975). Orientation over short distances (i.e., within a territory) often involves using objects (e.g., rocks, trees) to direct movements toward or away from such objects (i.e., guidance orientation); interpolating a return direction based on memory of landmarks or the perception of turns and the distances between turns [i.e., path integration (Etienne et al., 1986, 1991)]; and reliance on suites of objects and their configurations (Alyan and Jander, 1994). Exploration by captive rodents can lead to creation of a cognitive map of an arena (or maze) and use of this information for future decision making. As with food-caching data, this information is stored in the hippocampus of the brain (O'Keefe and Nadel, 1978). For a more general reference to cognitive maps, see Witschko and Witschko (1987).

At very large spatial scales (i.e., >100 km), cues emanating from or very near the goal cannot be perceived, at least during part of the journey. At such times orientation is performed using cues external to the goal (e.g., compasses based on the geomagnetic field, the sun, star patterns); cognitive maps navigating animals may use cognitive maps (or foraging, etc.). Individuals have multiple cues of orientation systems available to them, and these are not used in a simple hierarchical fashion (for problems involving conflicting and interacting cues, see Able and Able, 1995; Able, 1993). Weindler et al. (1996, 1997) manipulated wild birds in captivity and found they used both celestial and magnetic information for proper orientation. The magnetic compass (an inclination compass) provides information on the general direction to be taken in migration (Munro and Witschko, 1993), and celestial or other information refines the direction (Weindler et al., 1996). Homing pigeons (Columbia livia), well known for their orientation abilities (e.g., Beason et al., 1997), are often used for experiments at large spatial scales; these birds also have a well-developed capacity for orienting at small scales. Balda and Witschko (1995) trained caged homing pigeons to use their sun compasses as the basis for finding the spot at which a seed had been buried in a cup. Not only could the pigeons find the spot and retrieve the seed by digging for it; they could remember the locations of cups for as much as ten months.

The extent to which the same mechanisms are used for orientation in both long- and short-distance tasks is unknown. It should be noted that much prospecting probably occurs at spatial scales intermediate to those of laboratory setups and many bird migrations (e.g., Forbes and Kaiser, 1994; Switzer, 1993). Nevertheless, it is reasonable to pro-
pose that prospecting birds use mechanisms no different from some of those that birds rely on at these more extreme scales.

9. RELEVANCE OF PROSPECTING TO CONSERVATION BIOLOGY

The importance of the study of animal behavior to conservation biology has received inadequate attention (e.g., Clemmons and Buchholz, 1997). Below we discuss three areas in which understanding prospecting is relevant to conservation of birds.

9.1. Manipulating Habitat Quality

Given that prospecting for breeding sites is common if the cues birds rely on when they prospect can be identified, then it may be possible to manipulate those cues and thereby affect breeding distributions. Some recent conservation failures may have been caused by overlooking the potential importance of prospecting cues used by the birds involved (Kellner et al., 1992).

Using appropriate cues to manipulate behavior has been practiced by hunters for centuries, e.g., in attracting waterfowl by means of calls and decoys (e.g., Kear 1990). Along the same lines, nest boxes have been employed to attract cavity-nesting ducks (e.g., Wood Ducks, Aix sponsa) to areas from which they had been absent (e.g., Kadlec and Smith, 1982). Possibly the best example of applying this method purely for conservation purposes is the use of decoys to induce colonially nesting birds to establish new colonies. Kress (1983) presented painted decoys and played sound recordings of Least Terns (Sternula antillarum) to attract potential breeders to sites where he wanted colonies to form. The method also has assisted in starting colonies of Atlantic Puffins (Fratercula arctica) (Kress and Nettleship, 1988; Kress, 1978) and Laysan Albatrosses (Podolsky, 1990), and it may be generally applicable to colonial birds (Kress, 1997). Similar manipulations might be done by playback of conspecific song (Verner, 1992; Mountjoy and Lemon, 1991), or placement of old nests (Martos and Johnson, 1996; Yahner, 1993; Erckmann et al., 1990), or by supplying any other kind of information known or believed to be attractive to prospecting birds. Reintroduction of Griffon Vultures (Gyps fulvus) to former breeding sites in the Causses, France, was encouraged by spreading white paint to simulate droppings (Sarrazin et al., 1996). All these, and similar, methods could attract prospecting birds to newly created or restored areas. They also could be used to increase the size of small populations, assuming existing sizes were not the result of limitation of space or other resources (e.g., Sarrazin and Barbault, 1996). For example, some animals will not cross particular habitat types (e.g., Desrochers and Hannon, 1997; Rail et al., 1997; Caparella, 1988; Stamps et al., 1987), and others will not or cannot traverse long distances unless small stepping-stone-like patches of suitable habitat are present to serve as connections between two widely separated sites (e.g., Strong and Bancroft, 1994; Potter, 1990). In these situations, merely setting up reserves within the known dispersal distance for a particular species is inadequate.

9.2. Designing Reserves

There is much interest in supposed general rules about the design of reserves for species that occupy interior habitats (as opposed to edges). Among the most debated is the relative efficacy of large versus small reserves (e.g., Simberloff and Abel, 1976). Supposed general rules often are repeated but are rarely tested experimentally (see Noon and McKevey, 1996, for an exception). We doubt the value of generalized rules (particularly untested ones) and call attention to the truism that the decision about which reserve design is best for a particular species should depend on the species’ natural history. Knowledge of an animal’s behavior, including prospecting behavior, can be important to the reserve design (e.g., Woodroffe and Ginsberg, 1998; Villard and Taylor, 1994).

9.3. Effects of Prospect on Population Biology

Understanding how animals perceive and use their environment is critical for predicting the distribution and persistence of populations (Danchin and Wagner, 1997; Reed and Dobson, 1993; Wu et al., 1993; Hansen and di Castri, 1992; Hansson et al., 1992; Smith and Peacock, 1990; Stamps et al., 1987). Prospecting affects population biology by its potential role in dispersal, recruitment, and colonization. The consequences of preferential settlement patterns become clear with the study of metapopulations, i.e., sets of populations whose local dynamics are interdependent because of dispersal among them (Hanski and Gilpin, 1991; Levins, 1970; papers in McCullough, 1996; Gonzalez-Andujar and Perry, 1993; Wu et al., 1993; Hansson, 1991). Danchin and Wagner (1997), Reed and Dobson (1993), Ray and Gilpin (1991), and Smith and Peacock (1990), present models that show how the pres-
ence of conspecifics, which is a cue leading some prospectors to select breeding sites (see Section 9.1.), can affect population growth. And as described, manipulation of cues to suggest that conspecifics are present can even lead to the colonization of abandoned breeding sites.

If the distribution of cues attractive to prospectors is not random across an environment, then dispersal patterns will not be random. For example, if prospectors will not settle unless conspecifics are present in some minimum number, local recruitment rate will be affected and will differ from the standard (sigmoidal) growth pattern. And if dispersing members of colonially nesting seabirds are attracted preferentially to colonies with high reproductive output, then settlement patterns will be spatially biased across colonies. These potential differences in what makes a breeding site attractive, coupled with the multitude of ways in which a habitat can be fragmented (Lidicker and Koenig, 1996; Wiens, 1996), argue for the necessity of understanding dispersal behavior in order to predict and possibly manage population dynamics at local and landscape scales (Lima and Zollner, 1996). For example, restoring a habitat that is disjunct from similar habitats is a common conservation measure, particularly for wetlands (e.g., Haig et al. 1998). If individuals of a species that is intended to be attracted to occupy the new site explores in all directions and settles in all available habitat, the restored site will be colonized. However, if the individuals of the species do not prospect randomly (e.g., if they move along geographic contours) or if conspecifics must be present for a habitat to be acceptable, then the restored site may not be colonized.

9.3.1. Range Expansion

Prospecting has been shown in some species to play an important role in range expansion. Seabirds often are found outside their range, and they sometimes appear and breed in areas where they have not been recorded in the recent past (e.g., possibly Grey-faced Petrel, Pterodroma macroptera, and Black Petrel, Procellaria parkinsoni, McFadden, 1993; Juan Fernandez Petrel, Pterodroma externa, Imber et al., 1991; Leach’s Storm Petrel, Oceanodroma leucorhoa, Imber and Lovegrove, 1982).

In a review of the range expansion of the House Finch (Carpodacus mexicanus) in eastern North America, Viet and Lewis (1996) stated the leading edge of an expansion often was signaled by the appearance of a small number of individuals in an area, later followed by nesting and slow population growth. These leading birds (and their successors as the expansion continued), even though they were not individually marked and identifiable, probably fit our definition of prospectors searching for suitable breeding sites.

10. FUTURE RESEARCH

There are several interesting research directions: (1) Documentation of prospecting behavior needs to be continued. In particular, species that do not appear to engage in prospecting might be of special interest by considering the conditions in which the behavior would not confer a fitness advantage. (2) It is important to determine what differences, if any, exist in mechanisms of information storage and recovery and in orientation, at small (within-territory), intermediate (prospecting), and large (migration) spatial scales. This should create opportunities to manipulate cues important for settling and possibly, therefore, for conservation (e.g., Kress, 1978). (3) Modeling prospecting offers opportunities to understand the processes and consequences of dispersal and the behaviors involved in it; prospecting behavior should be incorporated into dispersal models, which should, in turn, predict its effect on population dynamics. Field studies should, of course, test the predictions of the models. (4) Research on hippocampal development of food-caching, homing (e.g., Shapiro and Wierszko, 1996), and migratory species raises important questions about prospectors. Are there differences in hippocampus size between prospecting and nonprospecting species, or among closely related species that rely on prospecting to different degrees? If so, what are those differences? Assuming prospecting differences are reflected in hippocampal differences and that the latter are affected by the individual’s experience, can change occur as a result of prospecting after a bird reaches adulthood?

A protocol developed to permit experimental investigation of prospecting under controlled conditions, as has been done repeatedly for foraging studies, would be a breakthrough in the study of this behavior. Captive experiments would require a fairly large enclosed area and would probably test small, nonmigratory birds that are nest-site specialists (such as cavity nesters). This would allow potential nest sites to be manipulated in order to yield a better understanding of prospecting decisions. Working on captive birds is not required, however, and exciting manipulative work has been done on free-living breeding-site specialists (colonial nesters: box-nesters: et al., 1998; Podolsky, 1990; Kress and Nettleship, 1988; Kress, 1978, 1983). For
both specialist and generalist nesters, field experiments involving deliberately displaced birds (e.g., Nolan and Kettridge, 1991; Kettridge and Nolan, 1990; Löhr, 1959) appear to be potentially strong research routes. If birds could be exposed to a single area, or to multiple areas that have been manipulated, the cues they use to select nesting sites or even nesting habitat could be demonstrated. It has been hypothesized that migratory birds prospect before autumn migration to develop a general area of familiarity or to select a specific future breeding location (e.g., Morton et al., 1991). This could be (and has been) tested experimentally in the field by displacing fledglings (Löhr, 1959, 1962) or postbreeding adults from their natal or breeding site and examining return rates the following year. Species showing strong philopatry or site fidelity are most likely to yield information. Such procedures could also be used to study hippocampal development, as has been done with food-catchers (see Section 8.2). If hypotheses exist regarding habitat quality, manipulating these factors or manipulating potential spatial (location) cues could be used to study settlement patterns of individually marked birds (Rosenzweig, 1991). For example, patterns of nest boxes or patterns of wetland locations could be manipulated. This desirable approach permits the exertion of minimum control over the experimental subjects, while mimicking natural conditions as closely as possible.

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