Gathering public information for habitat selection: prospecting birds cue on parental activity

Tomas Pärt[1*] and Blandine Doligez[2,3]

[1]*Department of Conservation Biology, The Swedish University of Agricultural Sciences, Box 7002, SE-750 07 Uppsala, Sweden*
[2]*Laboratoire d'Ecologie CNRS–UMR 7625, Université Pierre et Marie Curie, 7 quai Saint Bernard, Bâtiment A 7ème étage, Case 237, F-75252 Paris Cedex 05, France*
[3]*Institute of Zoology, Department of Evolutionary Ecology, University of Bern, Baltzerstrasse 6, CH–3012 Bern, Switzerland*

Because habitat quality strongly affects individual fitness, understanding individual habitat selection strategies is fundamental for most aspects of the evolution and conservation of species. Several studies suggest that individuals gather public information, i.e. information derived from the reproductive performance of conspecifics, to assess and select habitats. However, the behavioural mechanisms of information gathering, i.e. prospecting, are largely unknown, despite the fact that they directly constrain individual selection strategies. To test whether prospectors gather public information or other cues of habitat quality, we manipulated brood size of collared flycatchers (*Ficedula albicollis*) and investigated subsequent attraction of prospectors. Experimentally adding two nestlings increased the probability of attracting prospectors to the nest as a result of increased parental feeding rates. Prospectors were attracted to the most successful sites because feeding rate predicted subsequent fledgling production. In the year following prospecting, individuals selected a breeding site very close to the prospected site. These results provide the first experimental evidence, to our knowledge, of the links between information gathering behaviour and breeding habitat selection strategies based on public information.

Keywords: conspecific cues; dispersal; familiarity; feeding rate; information gathering; habitat quality

1. INTRODUCTION

Breeding habitat selection decisions may profoundly affect individual fitness and thus many aspects of the evolution and ecology of organisms (Cody 1985; Charlesworth 1994; Sutherland 1996). Understanding individual habitat selection strategies and the constraints acting upon them is therefore crucial for fundamental evolutionary and applied conservation purposes (Cody 1985; Sutherland 1996). Classical theoretical models of breeding habitat selection long assumed ideal conditions, where individuals have full knowledge of the relative quality of alternative breeding patches (Fretwell & Lucas 1970). In nature, however, individuals are likely to deviate from such ideal expectations because of (i) constraints acting on individual spatial knowledge and (ii) limited reliability of cues used in assessing habitat quality (Orians & Wittenberger 1991; Lima & Zollner 1996). Recent theoretical (Boulinier & Danchin 1997; Danchin *et al.* 2001; Doligez *et al.* 2003*a*) and experimental (Boulinier *et al.* 2002; Doligez *et al.* 2002) studies suggest that public information (i.e. information derived from the reproductive performance of conspecifics (Valone & Giraldeau 1993; Valone & Templeton 2002)), may be highly reliable information for selecting a breeding habitat, provided the environment is sufficiently predictable in time (Boulinier & Danchin 1997; Doligez *et al.* 2003*a*). However, to collect such public information, individuals need to prospect, i.e. to gather information about potential breeding patches (Reed *et al.* 1999; Danchin *et al.* 2001). Time and energy constraints on pros-

pecting behaviour will therefore determine which types of cue are available to individuals to assess measures of public information, which in turn may restrict the potential for such habitat selection strategies to be selected for in a given situation (see Giraldeau *et al.* 2002). Despite their crucial importance for the evolution of habitat selection strategies, the behavioural processes of gathering public information are nevertheless still unknown.

Empirical evidence that individuals prospect to gather public information is mainly limited to correlative studies and anecdotal observations of non-breeding individuals (in particular immatures and failed breeders) prospecting patches with actively breeding conspecifics at the time when they feed their young (Reed *et al.* 1999; Danchin *et al.* 2001). Such correlative evidence cannot be used to reject the alternative hypothesis that individuals gather other cues of habitat quality (e.g. vegetation structure (Orians & Wittenberger 1991) or presence of parasites (Boulinier *et al.* 2001)) that are linked to the reproductive success of conspecifics. A recent manipulation of the local reproductive performance of conspecifics in a population of collared flycatchers (*Ficedula albicollis*) showed that individual habitat selection is linked to public information (Doligez *et al.* 2002). This study further hypothesized that individuals use different measures of public information for settlement and departure decisions because of individual-specific constraints on information gathering behaviour (Doligez *et al.* 2002). However, although the use of public information was implicated in this study, the associated information gathering behaviour was not studied explicitly, thus leaving the results open to alternative mechanisms.

The collared flycatcher is a short-lived migratory passerine bird species nesting in tree cavities and nest-boxes.

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Prospecting flycatchers have been regularly observed during the nestling rearing phase of the breeding cycle, when they approach and inspect nest-boxes of conspecifics feeding their young (see Doligez *et al.* (2003*b*), see also Ottosson *et al.* (2001)). Correlative data on collared flycatchers indicate that the probability that prospectors are attracted to the nest increases with increasing parental feeding rate to the nestlings, suggesting that prospectors use parental activity to locate high-quality nesting sites (Doligez *et al.* 2003*b*). However, the direct links between prospecting behaviour, public information gathering and subsequent selection of a breeding habitat have not been shown experimentally in this or other species.

To test whether prospectors gather public information and to investigate the type of cues gathered, we experimentally manipulated individual reproductive success of collared flycatchers (*F. albicollis*) by increasing brood size, thus breaking up the links between conspecific reproductive performance and other cues of habitat quality. If flycatchers prospect to gather public information for breeding habitat selection in the next year, prospectors are expected to (i) be attracted to the most successful sites in the current year, i.e. nests with enlarged brood size, and (ii) settle preferentially near the prospected sites in the following year. If parental feeding rate is the cue used by prospectors, the probability of prospecting should increase at nests with enlarged brood size given that such a manipulation increases parental feeding rate. If other cues not related to public information are gathered, no difference in the probability of attracting prospectors is to be expected between enlarged and control nests.

2. MATERIAL AND METHODS

(a) *Study population, breeding data and brood size manipulation*

The main study was done in 1988 on a population of collared flycatchers breeding on the southern part of the Swedish island of Gotland (57°10′ N, 18°20′ E; for details see Pärt & Gustafsson 1989). Data on reproductive performance (date of egg laying, clutch size, number of nestlings and fledglings) and age of parents were collected using standard methods as a part of a long-term study on this population (Pärt & Gustafsson 1989). The brood size manipulation was performed by transferring two nestlings (7–8 days old) to randomly chosen (based on the age of breeding females (Pärt *et al.* 1992)) recipient nests. Each manipulated nest had a matched control randomly chosen among nests with the same hatching date and original number of nestlings. Feeding rates and prospecting activity were only recorded at nests with enlarged and unmanipulated broods. Controls and manipulated nests did not differ in laying date (*t* test: $t = 0.37$, d.f. $= 36$, $p = 0.712$), clutch size ($t = 1.59$, d.f. $= 36$, $p = 0.100$), age of male (Mann–Whitney *U* test: $z = 0.30$, $p = 0.765$) and female ($z = 0.09$, $p = 0.916$) parents.

(b) *Feeding rate to nestlings and prospecting*

Feeding rates of male and female parents were observed simultaneously for two matched nests during 3 h by two observers using telescopes from blinds 30–75 m from the nest-box. The observations were made between 0800 or 1200 and between 1300 and 1700 (Swedish summer time) when nestlings were 10 days old (Pärt *et al.* 1992). Prospecting birds ($n = 20$; 16 males and four females) were identified by the following criteria:

(i) presence near the nest of extra-pair individuals identified by colour–ring combinations and/or age (for males (Pärt 1994)): 77% of all classified prospectors; (ii) simultaneous presence near the nest-box (less than 2 m) of two individuals of the same sex: 55% of classified prospectors; and (iii) observations of individuals repeatedly inspecting nest contents from the nest-box entrance without entering (parents entered the nest-box directly when not disturbed): 41% of classified prospectors. Several of these criteria usually occurred together. Breeding pairs sometimes chased prospectors, but there was no difference in the frequency of chases among pairs with enlarged and control broods ($\chi^2 = 0.002$, d.f. $= 1$, $p = 0.96$). Because the parental feeding rate study was originally made for other purposes (Pärt *et al.* 1992), observers were unaware of the hypothesis tested here.

(c) *Breeding site choice of prospectors*

During the above observations, we identified three colour-ringed males that were found breeding in the subsequent year. To increase our sample of individually identified prospectors found breeding in the following year, we included all observations of individually colour-ringed prospectors visiting nests of pairs feeding nestlings between 1987 and 1990 (Pärt 1994, 1995). In total, nine individuals were identified (eight males and one female) and seven of them were known to have failed with their breeding attempt before prospecting. To test whether these individuals bred in year $t + 1$ closer to the site where they prospected than to their breeding site in year t, we compared straight line distances between all three locations. We recalculated dispersal distances in metres to distances in number of available territories (i.e. nest-boxes), excluding boxes occupied by early breeding tit species *Parus* spp. in year $t + 1$.

(d) *Statistical analyses*

Prospecting frequency and nestling survival data were analysed with multiple logistic regression, checking for overdispersion, and χ^2 values refer to likelihood-ratio χ^2. All logistic regression, ANOVA and ANCOVA models presented here were significant ($p < 0.05$). Logistic regression models were compared by using their Akaike information criteria (AIC) values: the model with the lowest AIC best fitted the data when AIC values differed by more than two (Burnham *et al.* 1995). Pooling the four female prospectors to data of male prospectors did not affect the results qualitatively compared with those based only on males.

3. RESULTS

(a) *Influence of nestling number and parental activity on the attraction of prospectors*

The brood size manipulation significantly increased mean number of fledged young by *ca.* 40% ($F_{1,36} = 21.1$, $p < 0.0001$). As a result of the increased number of nestlings in manipulated broods, parental food provisioning rates to nestlings increased by *ca.* 20% ($F_{1,36} = 7.16$, $p = 0.011$; figure 1*a*). Thus, we were able to manipulate not only the number of nestlings in the nest but also parental activity around the nest.

In line with the public information hypothesis, the probability of observing prospecting individuals was higher at enlarged broods compared with control ones ($\chi^2 = 6.56$, d.f. $= 1$, $p = 0.012$, accounting for date; figure 1*b*). The probability of attracting a prospector increased with parental feeding rate ($\chi^2 = 6.21$, d.f. $= 1$, $p = 0.013$; figure
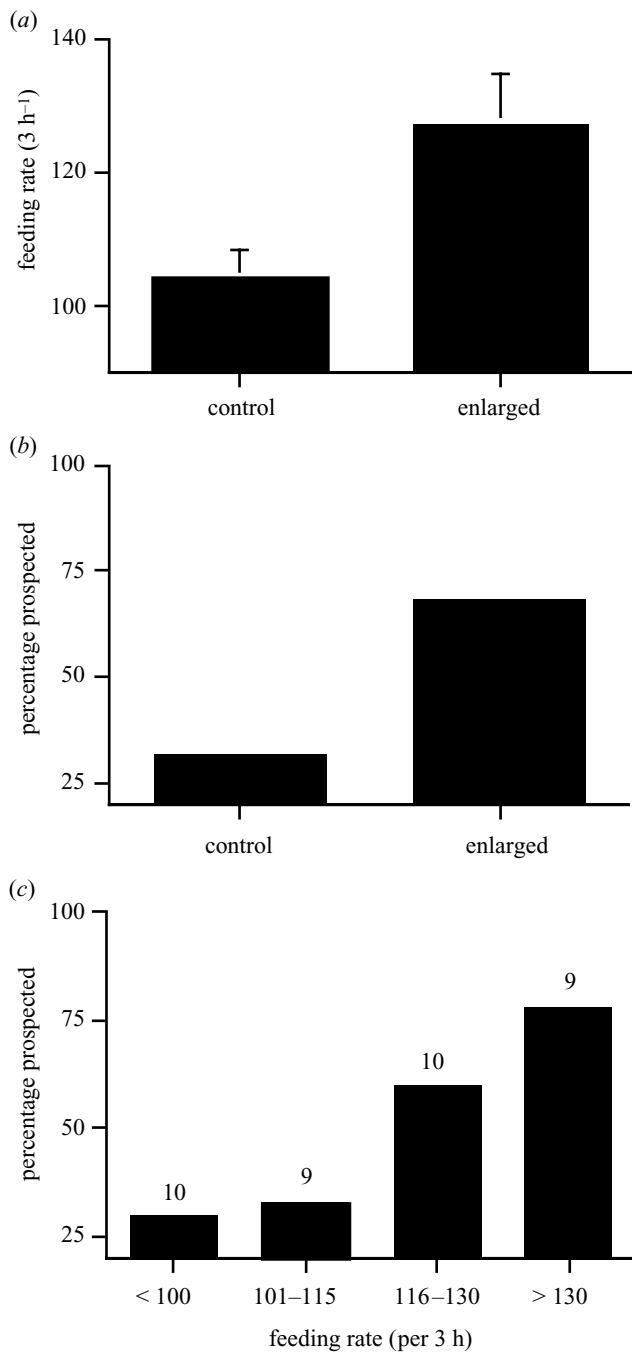
Figure 1. Effect of manipulation of brood size of collared flycatcher nests on (*a*) parental feeding rate to nestlings and (*b*) probability of being prospected by non-breeding or unsuccessful conspecifics (*n* = 19 nests in each group). The relationship between parental feeding rate and probability of being prospected is shown in (*c*) (sample sizes are shown above bars).

1*c*) while accounting for a general decrease in prospecting probability with time in the season ($\chi^2 = 4.46$, d.f. = 1, $p = 0.035$). The difference between enlarged and control broods in attracting prospectors was mainly caused by corresponding differences in observed feeding rate among experimental groups, as the model including feeding rate predicted prospecting frequency better (AIC = 48.5) than the model including nestling number (AIC = 51.9).

(b) *Parental activity as an indicator of local breeding success*

Feeding rate of 10-day-old nestlings was a predictor of nestling survival until fledging ($\chi^2 = 29.26$, d.f. = 1, $p < 0.0001$), and thus number of fledglings produced ($F_{1,34} = 9.71$, $p = 0.004$, accounting for manipulation and date in both cases). Therefore, parental activity around a nest is a good predictor of the reproductive success at fledging at that specific breeding site in the current year. Because reproductive success is locally temporally auto-correlated (Doligez *et al.* 1999), parental activity should also predict success at this site in the next year.

(c) *Prospecting and breeding patch choice in the next year*

Prospecting behaviour is linked to breeding site selection in the next year. All identified colour-ringed prospectors that were found again in year $t + 1$ (see § 2) bred closer to the nest site prospected in year t (median 80 m; range 0–300 m) than to the site where they attempted to breed in year t (median 369 m; range 72–2700 m; paired t test: $t = 2.77$, d.f. = 8, $p = 0.012$). All prospectors that changed woodland between their breeding attempt and prospecting (four individuals) bred in the following year in the woodland where they had been seen prospecting. The average distance moved between the prospected site and the next year's breeding site closely matched the average breeding dispersal distance of successful philopatric males (i.e. the sex with the most restricted dispersal; median distance 89 m; range 0–900 m (Pärt & Gustafsson 1989)), which shows that prospectors settled as close to their prospected site as successful breeders to their previous breeding site. In terms of territories moved, all prospectors bred within a distance of five territories (median: two territories) from the site where they were observed prospecting in the previous year. Five colour-ringed prospectors were repeatedly seen during several days (range: 2–10 days) within a very small area of less than six territories. Although the sample is limited, it clearly appears that prospecting is a behaviour aimed at identifying a high-quality future breeding patch based on public information measured by local parental activity.

4. DISCUSSION

Public information integrates the effect of all factors locally affecting breeding success (Danchin *et al.* 2001) and should thus be a reliable predictor of future success in different patches. Consequently, individuals could use public information for assessing quality of patches and selecting future breeding habitats (Doligez *et al.* 2003*a*). Such a strategy of breeding habitat selection requires that individuals prospect different habitat patches to gather cues of conspecific reproductive performance. The prospecting strategy that is selectively advantageous is likely to be determined by the availability of the various cues of public information and their power to predict future fitness. However, the benefits of using certain cues should be balanced with the costs of travelling and assessing information (e.g. owing to time and energy limitations, and intraspecific interactions). At present, such knowledge on prospecting behaviour and its relation to future selection of breeding habitats is lacking.

Our study is the first, to our knowledge, to experimentally show the links between prospecting behaviour, public information gathering and subsequent selection of breeding site. Prospecting collared flycatchers were probably attracted to enlarged broods mainly because parental feeding rates were higher at those than at unmanipulated broods (figure 1). Parental activity appears to be a general cue used to locate active nests not only by conspecifics, but also by nest predators (Martin *et al.* 2000) and brood parasites (Clotfelter 1998). Contrary to nestling number, i.e. a direct measure of current nesting success, parental activity is indeed conspicuous and easy to assess at distance. As in many other species (e.g. Maigret & Murphy 1997) parental feeding rate of flycatchers was related to the current brood value, measured by nestling number (see also Doligez *et al.* 2003*b*). More importantly, parental feeding rates predicted final production of fledglings and this holds true also in an unmanipulated situation (Doligez *et al.* 2003*b*). Prospectors could thus be attracted to the most successful nests by cueing on high parental activity. Because reproductive success is both temporally predictable and spatially autocorrelated at a local scale in this population (Doligez *et al.* 1999), prospectors may thus identify high-quality patches in which to breed in the next year. Our study indeed shows that collared flycatchers returned to breed in the close vicinity of the previous year's prospected site. Our observations furthermore suggest that prospectors stayed in a small area within a habitat patch during the prospecting phase. It is possible that such prospectors were acquiring local familiarity with the environment, which is selectively advantageous for territory acquisition and reproductive success in the next year (Pärt 1991, 1994).

The very fine cues used for selecting a future breeding habitat at a small spatial scale, as shown here for collared flycatchers, may be more common than currently known. A recent experimental study of a colonial species, where individuals breed in dense aggregations of nesting sites, and information on conspecifics is thus easy to gather (Danchin *et al.* 2001), suggests that individuals may prospect around active nests of conspecifics to subsequently select their breeding patch (Boulinier *et al.* 2002). Prospecting appears to serve this same purpose in species with spatially dispersed territories, as we show here. In general, gathering public information by prospecting may play a key role, particularly for sedentary species (e.g. sessile marine invertebrates) and species unable to move their eggs once laid (e.g. some insect, amphibian and fish species and most reptile and bird species), for which breeding habitat selection has dramatic consequences on fitness (Danchin & Wagner 1997). Such habitat selection strategies based on public information gathered by prospecting individuals may have profound consequences on animal distribution and dispersal (e.g. spatial aggregation of individuals (see Danchin & Wagner 1997; Wagner *et al.* 2000; Clobert *et al.* 2001)), but also on life-history traits (e.g. age at first breeding (Boulinier & Danchin 1997; Frederiksen & Bregnballe 2001)) and sexual selection (e.g. female mate choice in 'hidden leks' (Danchin & Wagner 1997; Wagner *et al.* 2000)). Investigating prospecting behaviour aimed at gathering public information for breeding habitat selection thus appears crucial for (i) understanding how spatial and temporal constraints on

information gathering shape evolutionary processes (e.g. imperfect choices (Real 1991; Holt & Barfield 2001)), and (ii) implementing efficient conservation strategies and management decisions (e.g. reintroductions or preservation of populations in small protected areas (Curio 1996; Caro 1999)).

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