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# Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting

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In long-lived bird species, a deferred onset of reproduction is assumed to be linked with a so-called prospecting phase when young individuals compare potential breeding sites before they decide to settle in the home area or to emigrate. However, this has rarely been documented with empirical data because of technical difficulties in collecting sufficient data from nonbreeding individuals at several sites. In the long-lived common tern, we used a novel transponder system to identify remotely all natal prospectors visiting two colonies of different size throughout the breeding season in 2001. Males attended the colonies about twice as frequently as females. Independently of sex, the proportion of birds recorded at both colonies was much higher among individuals born at the smaller colony. In the first half of their attendance time, individuals moved twice as often between colonies as in the second half. In both sexes, prospectors clearly favouring the larger colony were much more likely to breed there in the following season than prospectors with no clear colony choice, whereas no individual favouring the smaller colony during prospecting bred subsequently at the larger colony. Among birds born at the smaller colony, a higher proportion of female than of male prospectors attended mainly the larger colony, whereas among prospectors born in the larger colony, we did not find any sexual difference in attendance patterns and most birds favoured their home colony. The study suggests that prospectors select future breeding sites and that differences in philopatry between sexes are influenced by environmental quality.



From populations or subpopulations of animals, a certain percentage of individuals is assumed to emigrate to get access to resources on partners or to avoid inbreeding (Greenwood 1980; Hoeck 1982; Pusey 1987; Wolff 1993; Spear et al. 1998). This also allows small populations to remain viable (Andreassen & Ims 2001). In many species, one sex disperses at higher rates. The more frequently dispersing sex in mammals is the male and in birds usually the female; in general, it is the less territorial sex that disperses (Greenwood 1980). Animals are assumed to recognize habitat quality and dispersing individuals are thought to move mainly towards better conditions (Ims 1989; Brown & Brown 1992; Negro et al. 1997; Fasola et al. 2002; Pasinelli & Walters 2002). Most individuals disperse when young (Greenwood 1980; Dobson 1982; Hoeck 1982; Wolff 1993; Reed et al. 1999; Caizergues & Ellison 2002; Fasola et al. 2002; Serrano & Tella 2003).

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In long-lived bird species, a high percentage of young, but presumably mature, individuals attend potential breeding sites during the breeding season as so-called prospectors without starting a first breeding attempt in one or several years (Harrington 1974; Chabrzyk & Coulson 1976; Serventy & Curry 1984; Porter 1988; Ainley et al. 1990; Klomp & Furness 1990; Halley et al. 1995; Sarrazin et al. 1996; Dittmann & Becker 2003; Serrano & Tella 2003). Among other explanations for why these individuals do not breed directly, such as strong conspecific competition for suitable breeding sites (e.g. Wooller & Coulson 1977; Duncan 1978; Harris 1984; Hector et al. 1986; Coulson 1991; Gaston 1992) or a lack of skills (Curio 1983; Dittmann & Becker 2003), prospecting is probably a time when an individual compares potential breeding sites before deciding either to settle in the home area or to emigrate (Zack & Stutchbury 1992; Boulinier & Danchin 1997; Reed et al. 1999). The models of Boulinier & Danchin (1997) have shown that, in long-lived species, comparing sites and choosing a high-quality one may enhance total lifetime reproductive success even if this is linked with a later onset of reproduction. Although in many species males and females differ in dispersing



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behaviour (Greenwood 1980), nearly nothing is known about behavioural differences between sexes during prospecting, the time when the decision to emigrate is probably made. If during prospecting an individual prepares itself for future settling, we would predict the following behavioural traits as a consequence of the generally observed features of dispersing, as postulated in a similar way by Reed et al. (1999).

(1) The more frequently dispersing sex should be more mobile and visit more potential breeding sites. In consequence, attendance at a single site should be lower.

(2) For the decision either to settle in the home site or to disperse, the relative quality of the home site should be decisive. Attendance should be higher at a home site showing characteristics of high quality.

(3) If during the prospecting phase the birds select a future breeding site, the number of movements between sites might decrease and attendance at the selected site might increase over time.

(4) Birds should be more likely to breed at the sites they favoured during prospecting.

Empirical data indicating a spatial site selection among prebreeders are scarce, probably because of methodological problems in recognizing and observing sufficient numbers of nonbreeders throughout a season (Reed et al. 1999). In addition, most studies have been conducted at only one site. Little is known about a relation between a potential site preference during prospecting and the subsequent breeding site choice in the first year of reproduction although, on the smaller scale of subcolonies, some studies suggest that prospectors choose a place for breeding (Halley et al. 1995; Schjoerring et al. 1999).

Using an innovative transponder technique in the common tern as a model organism for a long-lived bird species, we identified automatically all natal prospectors from two colonies with different characteristics on the German North Sea coast at these two sites throughout the breeding season (Becker & Wendeln 1997). We assumed that one of the colonies was of higher quality because it was larger, which in general enhances the attractiveness of a site for colonial breeders (Ray et al. 1991; Spendelow et al. 1995; Brown & Brown 1996; Oro & Pradel 2000; Hernández-Matías & Ruiz 2003; Hernández-Matías et al. 2003; Martínez-Abraín et al. 2004), and further from the mainland (Becker & Anlauf 1988; Hernández-Matías & Ruiz 2003). At this site, reproductive success was higher during some years when breeding success was investigated equally at both colonies (unpublished data). For all prospectors, the sex was known. We recorded individual attendance patterns at both colonies throughout the season and compared them with breeding site choice in the following year.

## METHODS

The two colonies investigated were situated about 4 km apart in the harbour area of Wilhelmshaven, Lower Saxony, Germany. The colony site Banter See (BS, 53°27′N, 8°07′E) consists of six artificial islands of concrete. Each island measures 10.7 × 4.6 m and is surrounded by a low wall (60 cm high) equipped with 44 elevated places for the terns to land and rest on (resting platforms, Becker 1996; Becker & Wendeln 1997). The colony site Marinearsenal (MA, 53°52′N, 8°10′E) is an artificial island of concrete measuring about 13 × 2 m and is surrounded by a low fence (60 cm). The island was equipped with 11 elevated resting platforms. This study was part of an ongoing long-term population study conducted from 1992 to 2002 at BS and from 1997 to 2002 at MA. Owing to effective management to exclude rats, *Rattus norvegicus*, from the breeding site (Becker 1996), coupled with abundant food resources in the local environment, BS has, on average, a higher and more predictable breeding success per pair than MA and other colonies in the area (Becker et al. 1987; Becker 1998; personal observations) and we considered it to be a breeding site of higher quality. However, in the study year, the breeding success per pair was equal at both colonies. We show this in Table 1 together with other characteristics of both colonies which could have influenced the general attractiveness of the sites for new settling terns (Ray et al. 1991; Spendelow et al. 1995; Brown & Brown 1996; Oro & Pradel 2000; Hernández-Matías & Ruiz 2003).

Before fledging, we marked all chicks with metal rings and with subcutaneously injected passive transponders (Becker & Wendeln 1997) under licence of the Bezirksregierung Weser-Ems, Oldenburg (Tierschutzangelegenheiten). With these methods, we have marked chicks from 1997 to 2002 at MA and from 1992 to 2002 at BS. The transponders send an individual alphanumeric code when activated by special antennas placed on the resting platforms with a recording interval of 10 s. The system allows identification of birds for their whole life without retrapping (Becker & Wendeln 1997). No negative effects of this marking method on behaviour, adult survival or number of chicks fledged per pair have been observed (Wendeln & Becker 1998; González-Solís et al. 1999). To record the presence of marked birds during the breeding season, we used a system of antennas at the platforms from 1994 to 2002 at BS and in 2001 at MA. We distributed 35 antennas at BS and eight antennas at MA equally among the platforms and we changed their position regularly at intervals of 2–3 days to record the presence of marked birds with equal probability at all places. We recorded the presence of individual birds continuously throughout the breeding season from mid April until late August at BS and from 10 June until 23 August at MA. We checked the identity of all transponder-marked breeders by placing an antenna around each nest of the colony. We were therefore able to distinguish between breeders and nonbreeders. In 2002, the year after the prospecting studies, we identified breeders only at BS.

**Table 1.** Characteristics of the two common tern colonies investigated in 2001

| | Banter See (BS) | Marinearsenal (MA) |
|---|---|---|
| Area ($m^2$) | 295.3 | 26 |
| Distance from mainland (m) | 20 | 6 |
| No. of breeding pairs | 250 | 23 |
| No. of fledglings | 502 | 45 |

From 1998 onwards, we took some growing body feathers from all chicks aged about 14 days to sex them with routine PCR methods (Becker & Wink 2003). We defined as prospectors all 1–5-year-old individuals that were present in one or more consecutive years at one or both colonies and from which no breeding attempt was known so far (Dittmann & Becker 2003). We analysed only data from prospectors sexed since 1998. As about 83% of the common terns breed for the first time at age 3 or 4 after one or two seasons of prospecting (Ludwigs & Becker 2002; Dittmann & Becker 2003), we investigated prospectors of the typical ages in this study. At the colonies studied, most prospectors arrive in the third decade of June which is about 6 weeks after the mean arrival of experienced breeders (Ludwigs & Becker 2002; Dittmann & Becker 2003). We defined as recruits all transponder-marked birds that we recorded for the first time as breeders.

Figure 1 shows the attendance of a 2-year-old male and a 2-year old female prospector throughout the season at the two colonies. We defined the time elapsed from the first to the last data point as the total attendance time of a bird regardless of the colony at which we recorded the bird for the first and for the last time. To investigate whether individuals selected one of the sites during prospecting, we counted the moves between colonies in the first and in the second half of the total attendance time. In cases, where the total attendance time at the colonies was an unequal number of days, we defined the extra day as belonging to the first half. If the first registration of a bird in the second half of total attendance occurred at another colony than the last registration in the first half of total attendance, we defined this move as occurring during the second half. As the number of moves varied strongly between individuals, we calculated percentages of moves in the first and in the second half of total attendance. For analyses of moves between colonies, we used only birds attending both colonies with a total attendance time of at least 14 days.

We defined a day when a prospector was recorded at a colony as a 'registration day'. In this sense, a bird could reach a maximum of 2 registration days per day, if it was recorded at both colonies. We defined the sum of all registration days reached by a bird as 100%. We divided the proportions of registration days spent by the birds at BS into three classes of equal interval size. We defined prospectors as favouring BS if they spent 67% or more of all registration days at that site. Furthermore, according to this definition, prospectors showed no clear colony preference if they spent between 33 and 67% of all registration days at BS, and prospectors spending less than 33% of their registration days at BS (and, in consequence, more than 67% at MA) favoured MA. To avoid misunderstandings in the interpretation of the data, we emphasize that we use the terms 'colony selection', 'favoured colony' and 'colony preference' only with respect to the two colonies observed and in the given time intervals, as we had no information on whether and the extent to which the birds visited other colonies in the area.

To ensure that all birds included in the analyses had had equal probabilities of being recorded at both colonies, we used only data from birds that had arrived from 10 June onwards (80.7% of all prospectors in 2001, $N = 192$). For the same reason, we excluded data from single individuals recorded at BS after 23 August, the date when we removed the antenna system from MA after no bird had been recorded there for several days.

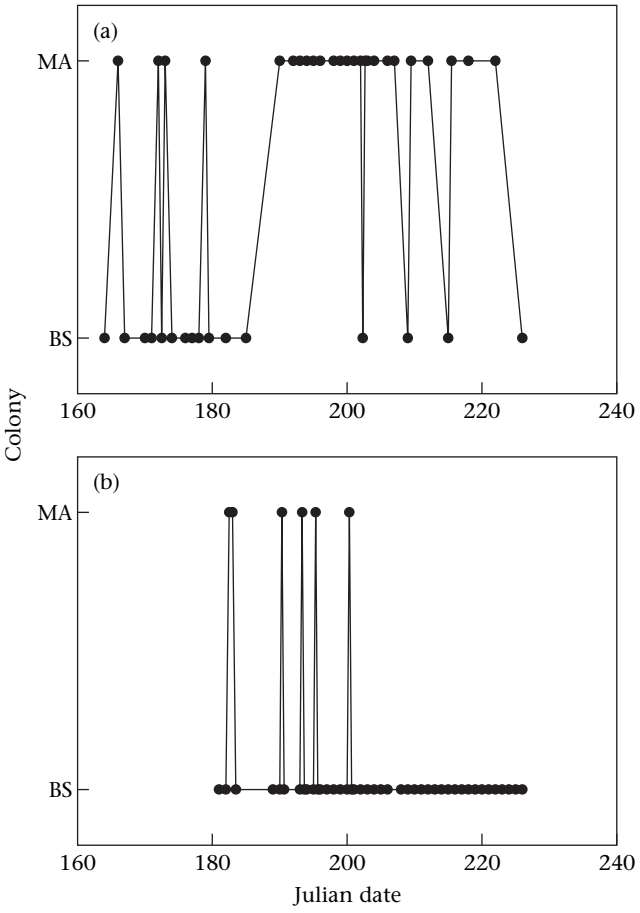


**Figure 1.** Attendance patterns of two prospecting common terns throughout the season at two colonies. (a) A 2-year-old male, (b) a 2-year-old female. The dots represent an individual's attendance at a colony on a single day. Diagonal lines indicate movements of the individual between the colonies (colony moves) regardless of whether the bird moved between colonies within or between days.

We performed all statistics with SPSS 10.0 (SPSS Inc., Chicago, IL, U.S.A.; level of significance $P \leq 0.05$). We give $P$ values for two-tailed tests of significance. We conducted all field work under licences of the Niedersächsisches Landesverwaltungsamt, Hanover, and of the Bezirksregierung Weser-Ems, Oldenburg (Nationalparkverwaltung).

## RESULTS

### Colony Attendance of Males and Females

Among prospectors born at BS, we recorded more registration days for males (median, interquartile range 36.75, 18.00–46.33, $N = 56$) than for females (11.00, 3.25–30.75, $N = 68$; Mann–Whitney $U$ test: $Z = -4.82$, $P < 0.001$). Similarly, among prospectors born at MA, males reached more registration days (38.50, 19.88–49.50, $N = 14$)

than females (13.00, 3.25–23.25, $N = 12$; $U = 28.50$, $P = 0.004$).

## Attendance Patterns of Natal Prospectors

Proportions of birds visiting, from the two colonies observed, only their colony of birth were significantly higher in birds born at BS than in birds born at MA, regardless of sex (logit-loglinear model: colony: $\lambda = 3.96$, $Z = 2.90$, $P < 0.01$; sex: $\lambda = 1.10$, $Z = 0.60$, $N = 150$, $P = 0.55$), whereas proportions of birds visiting both colonies and proportions of those recorded only at the foreign one were both lower.

## Moves Between Colonies

During the first half of attendance time, we counted nearly twice the number of moves between colonies as we did during the second half, regardless of sex (Fig. 2). In contrast, for both sexes, proportions of registration days did not differ significantly between the first and the second half (median, interquartile range males: first half: 51.28, 43.44–57.15; second half: 48.72, 42.85–56.56, $N = 37$; Wilcoxon test: $Z = -0.34$, $P = 0.73$; females: first half: 47.90, 28.75–57.71; second half: 52.10, 42.29–71.25, $N = 36$; $Z = -1.15$, $P = 0.25$).

## Favoured Colony

Among prospectors born at BS, a significantly higher proportion of individuals favoured their home colony for attendance (logit-loglinear model: $\lambda = 4.40$, $Z = 3.77$, $N = 150$, $P < 0.001$). Furthermore, a higher proportion of males than of females favoured their home colony (logit-loglinear model: $\lambda = 3.20$, $Z = 2.39$, $N = 150$, $P < 0.01$), but no mutual influence was detected between home colony and sex ($\lambda = -2.47$, $Z = -1.56$, $N = 150$, $P = 0.12$). However, when analysing birds from BS and MA separately, we found that a difference between sexes occurred only among prospectors from MA, with a larger proportion of males than of females favouring MA, coupled with a smaller proportion of males favouring the foreign colony, whereas similar proportions of males and females had no clear colony preference (Fig. 3).

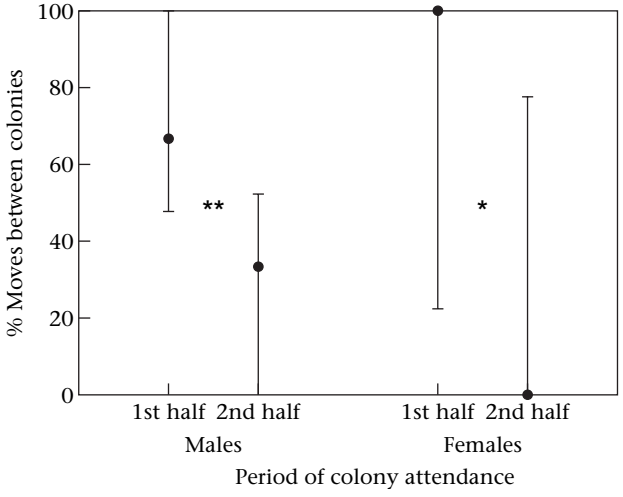


**Figure 2.** Percentage of moves of individual terns between two colonies in the first and in the second half of total attendance. Wilcoxon tests: *$P < 0.05$; **$P < 0.01$. Medians are shown with the interquartile range. $N = 37$ males, 36 females.

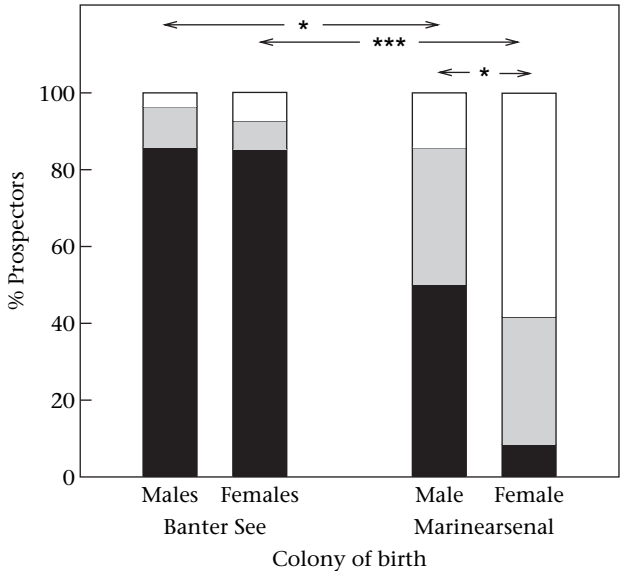


**Figure 3.** Percentage of sexed native common tern prospectors from two colonies favouring their home, none or the foreign colony. Crosstabulations: *$P < 0.05$; ***$P < 0.001$. Favoured colony: ■: home colony; ▨: undecided; □: foreign colony. $N = 56$ males, 68 females at Banter See and 14 males, 12 females at Marinearsenal.

## Future Breeding Colony

In both males and females, the probability of recruitment at BS in 2002 decreased significantly with a decreasing proportional colony attendance when prospecting at BS in 2001, whereas the sexes did not differ in recruitment probability (logistic regression: proportional colony attendance: Wald $\chi^2_1 = 10.370$, $P = 0.001$; sex: Wald $\chi^2_1 = 0.07$, $N = 150$, $P = 0.80$; Fig. 4).

# DISCUSSION

The high proportion of natal prospectors visiting both study colonies regardless of their colony of birth supports the hypothesis that individuals should use their prebreeding period for comparing different potential breeding sites (Serventy & Curry 1984; Porter 1988; Ainley et al. 1990; Rosenzweig 1991; Zack & Stutchbury 1992; Boulinier & Danchin 1997; Danchin & Wagner 1997; Reed et al. 1999). On the other hand, for both colonies and for both sexes, we recorded a certain percentage of prospectors only at the natal or only at the foreign colony. The fact that the percentage of individuals visiting only the natal colony was much higher in the larger colony, coupled with a lower proportion of prospectors born at the larger

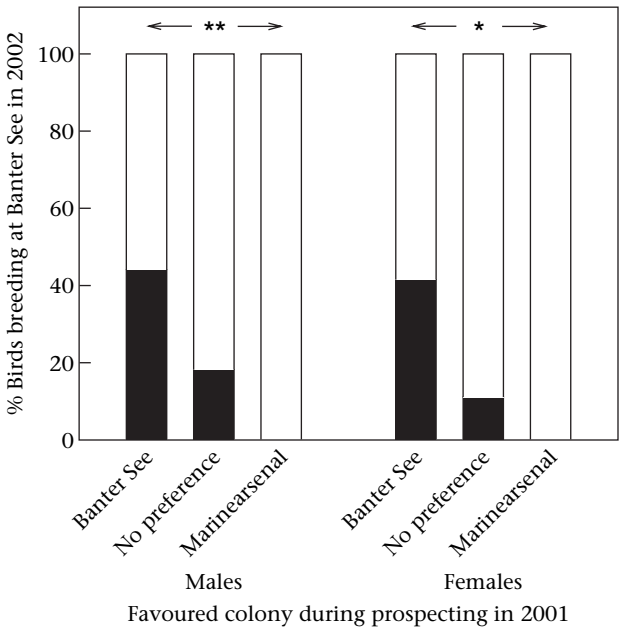


**Figure 4.** Percentage of sexed prospectors of 2001 recruiting at Banter See in 2002 (■) with respect to which colony they favoured in 2001. Crosstabulations: *$P < 0.05$; ***$P < 0.001$. Males: $N = 50$, 11, 9; females: $N = 65$, 9, 6, recruiting at Banter See, no preference and recruiting at Marinearsenal, respectively.

colony recorded only at the smaller colony, resembles the findings for different colonial breeders among both mammals and birds, including the common tern, for which larger colonies are more attractive (Hoeck 1982; Kotliar & Burger 1984; Ray et al. 1991; Spendelow et al. 1995; Brown & Brown 1996; Oro & Pradel 2000; Fasola et al. 2002; Forero et al. 2002; Serrano & Tella 2003). In the studies cited, however, most or all individuals observed were breeders. Because we studied prospectors, which are assumed to be mobile and motivated to compare different potential breeding sites, as mentioned above (Boulinier & Danchin 1997; Reed et al. 1999; Fasola et al. 2002; Dittmann & Becker 2003), conspecific attraction alone does not explain sufficiently why a high percentage of individuals born at the larger colony were never recorded at the smaller site. Because the colonies were close enough for many birds from the larger colony to overfly the smaller site on their way to the feeding grounds in the Wadden Sea (personal observation), it seems unlikely that the birds were not recorded at the small, and therefore probably less conspicuous, colony because they failed to find it.

Boulinier & Danchin's (1997) model shows that, under certain conditions, in a long-lived bird species, prospecting may be better than breeding if high-quality sites are scarce. Nevertheless, further prospecting may not be profitable if a high-quality site, the home site, has already been found. We assume that the observed differences in general attendance of natal prospectors from two colonies of different quality reflects a trade-off between the cost of exploring further colonies and the chance of finding a better place, as suggested in a similar way by Schjoerring (2002). However, this hypothesis implies that birds are able to assess 'absolute' breeding site quality. As the process of recognizing environmental quality in birds is poorly known (Reed et al. 1999), this remains speculative.

When we observed not only where individuals of the two colonies were recorded in general, but also how long they spent at which colony site, we found that most individuals clearly favoured one colony. In addition, the proportions of prospectors born at the large colony that favoured the small colony were much smaller in both sexes than the proportions of prospectors born at the small colony that attended mainly the large one. This finding supports the hypothesis of conspecific attraction mentioned above (Kotliar & Burger 1984; Ray et al. 1991; Spendelow et al. 1995; Brown & Brown 1996; Oro & Pradel 2000; Fasola et al. 2002; Forero et al. 2002; Serrano & Tella 2003).

If, after comparing different colonies, prospectors finally select a specific site (Boulinier & Danchin 1997; Dittmann & Becker 2003), we would predict that, besides a higher attendance at a favoured site, the number of individual moves between colonies (Fig. 1), should decrease. Supporting this prediction, we found for both sexes significantly fewer moves in the second half of an individual's attendance time. Similarly, Halley et al. (1995) interpreted a lower number of subcolonies visited by older prospectors as indicative of an increasing fidelity to a certain selected site. In our study, the proportions of individual registration days did not differ between the first and the second half, so we can exclude for both sexes that the fewer moves observed solely reflected a lowered general colony attendance.

As we interpreted prospecting as a period during which a site is chosen, we expected to find certain similarities between attendance patterns during prospecting and the choice of the first breeding site in the following season. We found that prospectors favouring the colony BS in 2001 were significantly more likely to start a first breeding attempt there in 2002 than individuals favouring colony MA or than individuals that did not show a clear colony choice. Unfortunately, as the identity of breeders at MA was not recorded in 2002, we were not able to record the complementary situation. The positive relation between colony attendance when prospecting at BS in 2001 and recruitment probability at BS in 2002 corresponds to the observation that, even on the small scale of subcolonies, high percentages of terns recruit at places they had mostly attended during prospecting in the previous season. (T. Dittmann & P. Becker, personal observation). A positive relation between attendance at a site and subsequent breeding probability has also been reported by other authors (Cadiou et al. 1994; Halley et al. 1995; van der Jeugd 2001). We conclude that prospecting terns choose a future breeding site. As a consequence, it should be possible to predict a bird's readiness to settle at a site for breeding or to emigrate from its attendance pattern during prospecting.

When we compared the attendance patterns of males and females with respect to their natal colony, we observed that, among natal prospectors from the small

colony, females were significantly more likely to favour the foreign colony than males. This is in accordance with the general observation in most birds that, if a sexual difference in philopatry is found, males are more philopatric than females (Mills 1973; Chabrzyk & Coulson 1976; Greenwood 1980; Coulson & Nève de Mévergnies 1992; Clarke et al. 1997). This fact has often been explained by males investing more in defending a future nesting territory, which is also true for the common tern (Wiggins & Morris 1987; Wendeln 1997), coupled with higher benefits from an already well-known environment (Großkopf 1970; Nisbet 1973; Greenwood 1980; Glutz von Blotzheim & Bauer 1982; Wiggins & Morris 1987; Weimerskirch 1992; Ristow 1998; Borg 1999; González-Solís et al. 1999). In contrast, for females it might be more important to find a male with a nest territory (Reed & Oring 1992; Reed & Dobson 1993). This resource should be more abundant within a large colony; a higher availability of potential partners is sometimes considered as one advantage of colonial breeding in general compared with single breeding (Wittenberger 1983; Draulans 1988), if there are more potential mates in a large foreign colony, leaving a small home colony might be profitable. The higher average attendance in male than in female prospectors at the home colony can be interpreted in the same way. In contrast, among prospectors native to the larger colony, we did not find any difference in favoured colonies between the sexes. We assume that, owing to the high quality of the colony BS (high breeding success, a high density of conspecifics as potential mates and greater protection against predators), many female terns gave up extensive prospecting at other sites in favour of settling at BS.

The apparently lower investment in prospecting at other places corresponds to the findings in several other studies where emigration distances were lower than expected as an adaptation of behaviour to a high site quality (Doherty et al. 2002; Pasinelli & Walters 2002). Similar to the attendance patterns of prospectors in our study, Danchin & Monnat (1992) and Danchin et al. (1998) reported a higher dispersal rate from a lower quality habitat, probably in part as a consequence of previous prospecting activity. Winkel (1981) found a high dispersal rate of coal tits, *Parus ater*, in particular of females in a young forest, whereas Dietrich et al. (2003) found a lower dispersal in general, with equal dispersal rates of the sexes, in the same forest with older trees, forming a more favourable habitat. We believe that, to estimate the degree of difference in dispersal rates between the sexes of a species, a detailed knowledge about habitat quality in the population studied is crucial. However, in our study, females from both colonies were recorded during fewer days than males. This indicates that females were more often absent from the colonies observed and probably visited other colonies in the surroundings where registration was not possible. In turn, the finding underlines the generally greater importance of presence at a colony for males, regardless of habitat quality.

The obviously higher willingness to emigrate in birds of both sexes from the smaller colony also supports the hypothesis that emigration is an important mechanism to avoid inbreeding in a population (Greenwood 1980; Dobson 1982; Pusey 1987; Wolff 1993). In theory, among patchy populations, for example colonies, the necessity for an individual to leave the colony should be higher in smaller colonies with less chance of finding an unrelated mate. For this reason, in animals with sex-biased emigration rates, one would predict a higher emigration rate from small colonies of the more frequently dispersing sex, the female in the majority of seabirds (Mills 1973; Chabrzyk & Coulson 1976; Greenwood 1980; Coulson & Nève de Mévergnies 1992; Clarke et al. 1997). In support of this prediction, we found a corresponding difference between the sexes in colony preference before dispersal only in terns born at the small colony. In practice, a higher emigration from smaller populations may, on the one hand, be profitable for an individual's fitness but, on the other hand, it may enhance the risk of extinction of small populations, as suggested by Andreassen & Ims (2001), which might be important for species conservation in fragmented habitats.

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