Within and between season nest-site and mate fidelity in Common Terns (*Sterna hirundo*)

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Summary

We studied nest-site and mate fidelity in renesting Common Terns (*Sterna hirundo*), from 1993 to 1997, in a Common Tern colony breeding on six small artificial islands in the harbour area in Wilhelmshaven (German North Sea coast). Implanted transponders made possible individual recognition of the adults throughout their lifetime. We compared intra-season rates of nest-site and mate fidelity with between-year rates. Intra-season divorce was never observed. On the other hand, inter-year divorce was estimated at about 25%, suggesting that the costs of intra-season divorce are higher or opportunities for divorce are lower than between years. For 75% of 26 pairs that renested within the same season, the distance moved was less than 4.3 m. For 75% of 57 faithful pairs between two consecutive seasons, the distance moved was less than 1.25 m. Dispersal distances between and within years did not differ significantly but were clearly shorter than a paired random distribution of nests. Most of the birds changed the nest-site either when renesting or between years, but most of the new scrapes can be considered as lying within the original territory. Thus, failure of the first breeding attempt increased neither divorce nor nest-site dispersal as compared with between-year rates. We also studied the influence of parental age and the date of breeding failure on distances moved in renesting birds. Late renesting pairs did not change the nest-site. A multiple regression analysis revealed that the longer the duration of the first breeding attempt and the older the pair, the shorter the nest dispersal distance.

Key words: age, breeding failure, divorce, nest dispersal, renesting

Zusammenfassung

Neststandort- und Partnertreue ersatzbrütender Flußseeschwalben (*Sterna hirundo*)

Von 1993–1997 untersuchten wir Neststandort- und Partnertreue ersatzbrütender Fluß-seeschwalben (*Sterna hirundo*) in einer Kolonie, die im Banter See, Wilhelmshaven, auf sechs künstlichen Inseln brütet. Transponder ermöglichten die lebenslange individuelle Erkennung der Altvögel. Neststandort- und Partnertreue innerhalb der Brutsaison und zwischen den Jahren wurden verglichen. Innerhalb der Brutsaison kam Scheidung nicht vor. Eine Trennungsrate von 25% zwischen den Jahren deutet darauf hin, daß die Kosten einer intrasaisonalen Scheidung höher sind als die diejenigen einer Scheidung zwischen den Jahren. 75% der ersatzbrütenden Paare wählten den neuen Neststandort weniger als 4,3 m vom Platz des Erstgeleges entfernt (n=26). 75% der partnertreuen Paare brüteten

im Folgejahr nur 1,25 m entfernt vom Neststandort des Vorjahres (n = 57). Die Entfernungen zum Neststandort des Folgegeleges innerhalb und zwischen den Jahren unterschieden sich nicht signifikant, waren aber deutlich geringer, als nach einer Zufallsverteilung zu erwarten war. Die meisten Flußseeschwalben wechselten den Neststandort bei einer Ersatzbrut oder im Folgejahr, aber meist wurde das folgende Gelege im ursprünglichen Territorium angelegt. Folglich führt ein Verlust der Erstbrut weder zu erhöhter Scheidungsrate noch zu stärkerer Verlagerung des Neststandorts, verglichen mit der Situation zwischen Jahren. Auch der Einfluß des Alters und Termins des Brutverlusts auf die Distanzen zwischen Erst- und Ersatzgelege wurden untersucht. Späte ersatzbrütende Paare verlegten ihren Neststandort nicht. Eine multiple Regressionsanalyse verdeutlichte, daß die Distanz zum Ersatz-Neststandort abnimmt, je länger der erste Brutversuch andauerte und je älter das Paar war.

Introduction

Nest-site fidelity, the tendency to nest in the same place within the colony-site every year (McNicholl 1975, Macdonald 1977), is known to be affected by previous breeding success (e.g. Ollason & Dunnet 1978, Coulson & Thomas 1980, Aebischer et al. 1995). The local knowledge of the colony-site with respect to flood or predation risks is usually thought to promote fidelity to the nest-site (Nisbet & Welton 1984, Becker & Anlauf 1988). In predictable habitats, however, moving to another site may be favoured after a breeding failure (Switzer 1993).

The study of partnerships in birds has recently attracted much attention (Black 1996). Although divorce appears to be weakly related to previous breeding failure, at least four hypotheses predict an increased tendency to divorce after a breeding failure: the incompatibility hypothesis; the better option; the errors of mate choice; and the habitat mediated hypothesis (see Choudhury 1995, Ens et al. 1996 for reviews). To put it in a nutshell, breeding dispersal and divorce may be increased by previous breeding failure.

Changes in dispersal and pair bond status have been extensively studied between one breeding season and the next (see reviews in Greenwood 1980, Black 1996). Relatively little emphasis has been placed on within-season site and mate fidelity (but see Greig-Smith 1982, Shields 1984, Lifjeld & Slagsvold 1988, Slagsvold & Lifjeld 1990, Hepp & Kennamer 1992, Cezily & Johnson 1995 for some exceptions), and especially so in seabirds. In accordance with the results found for nest-site and mate fidelity between years, increased breeding dispersal and divorce rates could be expected when birds renest after a first breeding attempt has failed. However, short-term changes in food resources, predation risk, or quality of available nest-sites and mates can occur as the breeding season progresses. These changes are likely to influence the equilibrium between costs and benefits of both nest-site and mate fidelity. Therefore, within-season selective pressures can differ from those between years and may affect strategic reproductive decisions of birds.

Common Terns Sterna hirundo show a high degree of mate and nest-site fidelity (Austin 1947, González-Solís et al. 1998, in press). However, within-season studies on pair bond status and dispersal between nest and renest attempts are lacking. Its breeding cycle usually comprises one breeding attempt per year, although some birds are able to renest when the first breeding attempt has failed (González-Solís et al. 1999). If an external disaster strikes the colony so that all birds fail, the entire colony usually moves to a new breeding area. However, if only few birds from the colony are involved in the breeding failure, the majority produce a replacement clutch at the same colony-site (Austin 1949, 1951). Here, we studied Common Terns renesting in the same colony.

We compared intra-season and inter-year nest-site dispersion distances as well as rates of divorce. We also analyzed the influence of parental age and date of breeding failure on breeding dispersal between first nest and renest attempts.

Methods

We carried out the field work from 1993 to 1997 in a Common Tern colony site at "Banter See" in Wilhelmshaven (German North Sea coast). About 150–250 pairs breed regularly on six artificial islands. The islands are stable, flat and rectangular, of equal size (10.7 x 4.6 m) and the distance between islands is around 0.9 m. From 1992 to 1997, we fitted transponders to 101 adult Common Tern breeders as well as to all fledged chicks. The transponder allow an individual identification of the adults at the nest-site (described in detail in Becker & Wendeln 1997). Since 1993, we have been checking each nest for individuals bearing transponders by placing an antenna at the nest during the incubation period for 1–2 days. In 1997, 118 breeders were identified. Every year, we marked each nest by a stick and its position was recorded once the breeding season was finished. We ascertained the fate of the eggs and chicks from colony checks every two or three days during the breeding period (Becker and Finck 1985).

We selected those pairs where both mates carried transponders for calculating the intra-season and inter-year divorce. For calculating the renesting dispersal of a pair, we used all the pairs where one or both birds carried a transponder, since no intra-season divorce was observed. We considered as renesting birds only those that produced a replacement clutch after their first breeding attempt had failed. Thus, we did not consider as renesting birds interrupted clutches finished in a second nest-site and second clutches after fledging chicks. The age of many adults was known because they were ringed as chicks. As ages of the mates are highly positively correlated (Nisbet et al. 1984; Neubauer 1997, this study $r2 = 0.77$, $n = 22$, $P < 0.0001$, range 0–6 years, mean difference = 1.0 year), we estimated the age of the pair as the age of one of the mates or the average age of the two if both were known. Information on age was lacking for some pairs; therefore, sample sizes were lower for those analyses that included this variable.

We defined the inter-nest distance (IND) as the distance between nest- and renest-sites within each season or between nest-sites of two consecutive years. IND was calculated as a straight line distance between nest-sites for each individually identified pair. We defined the laying date of the first breeding attempt (LD) as the number of days elapsed from the first of January to the date when the first egg was laid for the respective year. We defined the duration of the first breeding attempt as the number of days elapsed from the laying date to the loss of the last egg or chick of this first clutch. We defined the renest interval as the number of days elapsed between the loss of the last egg or chick of the first clutch and the laying date of the first egg of the replacement clutch. A pair was considered divorced when both marked parents were known to be alive but did not make the next breeding attempt together. We defined a pair as having inter-year divorce when a pair split up between the last breeding of one year and the first breeding attempt of the following year. We defined a pair as having intra-season divorce when a pair split up between the first breeding attempt and the renesting attempt of the same season.

In order to correct and homogenise for inter-annual variability and to allow pooling of data, we obtained the residual laying date (RLD) by subtracting each annual average laying date from the individual value in that year. We performed a logarithmic transformation on inter-nest distance (IND) to approach normality and variance homogeneity. We carried out a stepwise multiple regression analysis on IND with the RLD, the duration of the first breeding attempt, the renest interval and the logarithmic value of the age of the pair, to determine which of these variables influenced IND significantly. Since age was missing for some cases, we used pairwise treatment of missing values. We examined the multiple regression for normality.

Results

In a group of 57 faithful pairs, for 75% of them the distance moved between two consecutive seasons was less than 1.25 m, which can be considered a distance within the original territory (median distance moved = 0.80 m). For 26 pairs renesting pairs, the distance moved for 75% and 50% of the pairs within the same season was less than 4.3 m and less than 1.17 m,
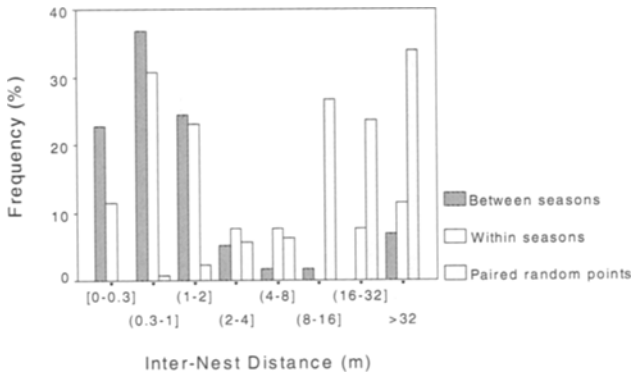
respectively. Figure 1 shows a histogram of the distances moved between and within seasons as well as the distribution of distances of 10,000 paired random points. Differences in distances moved within and between seasons were not significant (t-test for unequal variances on log-transformed IND: $t = -0.85$, $df = 33$, $p = 0.4$). Since previous reproductive success might affect dispersal distances, we repeated the same analysis excluding faithful birds that did not fail the preceding season. In this case, dispersal distance within years was not significantly different than between years (t-test on log-transformed IND, $t = -0.47$, $df = 32$, $p = 0.6$). Likewise, we performed a paired t-test for faithful pairs with known dispersal distances within a year as well as between the renesting year and the precedent year. Of those pairs, differences in dispersal distances within and between years were again not significant ($t = 0.75$, $df = 12$, $p = 0.5$). Pairs that renested were significantly older than pairs that did not renest (Table 1, t-test on log-transformed age: $t = -2.31$, $df = 207$, $p < 0.05$). From those pairs that renested, 3 renested in the same nest-site and 23 changed nest-site. Birds that did not change nest-site for renesting showed a significantly longer duration of the first breeding attempt than those birds that changed ($U = 4.5$, $n = 26$, $p = 0.01$).

Multiple regression was performed for those renesting terns that changed nest-site within a year. The sample size was 23 for all the variables except for age ($n = 15$). Only the duration of the first breeding attempt ($B = -0.038$) and the age ($B = -3.986$) improved the multiple regression with IND significantly ($F = 7.69$, $df = 2,12$, $r^2 = 0.57$, $p < 0.01$). Although the residual laying date of the first breeding attempt was significantly correlated with the inter-nest distance and with the age (IND-RLD: $n = 23$, $r = 0.54$, $p < 0.01$; Age-RLD: $n = 15$, $r = -0.58$, $p < 0.05$), residual laying date did not improve the regression significantly. Older pairs renested closer to the first nest-site than younger pairs. Simultaneously, pairs with longer duration of the first breeding attempt renested closer to the nest-site of the first breeding attempt than pairs with shorter duration.

Of 95 checked pairs with both mates fitted with transponders, 24 (25 %) showed inter-year divorce. However, among the 17 renesting pairs with both mates fitted with transponders, none showed intra-season divorce. Differences between inter-year and intra-season divorce rate were significant ($G = 6.54$, $df = 1$, $p = 0.01$). There was no significant differences in the average age between inter-year faithful and divorced pairs (Table 1, t-test on log-transformed age: $t = -0.55$, $df = 63$, $p = 0.6$).

Table 1. Average age and standard error for Common Tern pairs depending on renest and inter-year pair bond status. n = sample size. s.e. = Standard error.
Tab. 1. Mittleres Alter (Jahre) von Flußseeschwalbenpaaren in Abhängigkeit von Partnerbindungs- und Ersatzbrut-Status. n = Stichprobengröße. s.e. = Standardfehler.

	n	Age Alter	s.e.
Faithful partnertreu	53	8.13	0.41
Divorced geschieden	12	9.16	1.21
Do not renest keine Ersatzbrut	191	7.14	0.26
Renest Ersatzbrut	18	7.94	0.55

Discussion

Renest dispersal

Nest predation has been reported as a major cause of losses in birds (Ricklefs 1969, Martin 1993, Becker 1998). Colonial seabirds feed outside the nesting area, hence, the quality of the territory is mainly a factor of intensity of predation. In seabirds, vulnerability to predators depends greatly on the position of the nest-site (Götmark & Andersson 1984, Becker 1995). In our colony, renesting birds lost their first clutch or brood mainly through owl and rat predation. After a first breeding failure, birds may change the nest-site in order to renest in a better quality nest-site. However, most of the birds that renested changed the position of the nest-site to the same extent as between years. Although most of the birds changed the position of the nest, the distances between the first and second nest were clearly shorter than those expected of a random distribution, and new scrapes were usually in the same territory as the first breeding attempt. Similar results were reported by Arnold et al. (1998) for a Common Tern colony at Bird Island (Massachusetts, USA), where 50% (n = 16) of renesting pairs used the same territory for renesting after egg removal of the first clutch. Thus, predation of the first breeding clutch or brood when restricted to few nests does not affect nest dispersal of the second clutch.

Dispersal within the same season seems to be constrained by the time available for renesting. Our results show that dispersal distance decreases with the duration of the first breeding attempt. One reason for this may be the need to synchronise hatching with the rest of birds in the colony in order to reduce predation (e.g. Gochfeld 1980). Moreover, some studies reported a decreased ability to renest (Parsons 1976, Wooller 1980, Storey 1987) and also decreased breeding success with the advancing season (Sydeman et al. 1991), suggesting that birds should renest as soon as possible after a breeding failure. Resettling into a new territory would imply new competitive interactions with new and more neighbours (Burger & Gochfeld 1991) and could considerably delay the renesting date. Thus, renesting in the same territory may be a strategy to save time, especially for late renesting birds.

Older renesting terns tended to renest closer to the first nest-site than younger terns. Birds will disperse after a breeding failure when they have the chance to get a better quality nest-site. This chance, however, is thought to depend on the quality of available nest-sites other as well as on the quality of the original one. Older birds are the first individuals to arrive to the colony-site and choose higher quality nest territories than younger birds (Potts et al. 1980, Wooller 1980, Pugesek & Diem 1983, Nisbet et al. 1984). The probability of obtaining a bet-

ter nest-site in a new territory would thus decrease with age and therefore, shorter dispersal distances for old birds than for young birds can be expected.

Intra-season and inter-year divorce

It would seem to be of greatest advantage for a bird to divorce if the reproductive success with the same mate is less than the expected success with a new mate. This could be extended to imply that pairs are more likely to divorce after a breeding failure, as shown in some species for inter-year divorce (see review in Ens et al. 1996). Within a season, an increased divorce rate after nest failure and before a renest attempt could be also expected. However, whilst the divorce rate between years was about 25%, none of the pairs divorced between nest and renest attempts. Similarly, in Caspian Terns (*Sterna caspia*) inter-year divorce occurred in about 75% of the pairs, in contrast with no divorce in 5 renesting pairs (Cuthbert 1985). The same phenomenon was observed for Least Terns (*Sterna antillarum*): Only in two of 90 renests was the formation of a new mid-season bond observed, and the new pairs were formed, presumably, because in both instances the first mate disappeared after the first clutch hatched (Massey & Fancher 1989). In Sooty Tern (*Sterna fuscata*) none of 6 pairs split up before relaying (Ashmole 1963).

Intra-season divorce could be lower through the effect of age. Renesting pairs are usually older than non-renesting ones and older pairs show a lower tendency to divorce than younger ones (Coulson & Thomas 1980, Ens et al. 1996). In this study, renesting pairs were only slightly older than non-renesting pairs. Moreover, there was no significant difference in average age between inter-year divorced and faithful pairs. Thus, our results suggest that the bias in the age of renesting pairs was not related to the absence of intra-season divorce.

Birds that fail their first breeding attempt are thrown back in the season compared to those birds that arrive in the colony at the start of the breeding season. Thus, selective pressures within years can differ from those which obtain between years and alter the equilibrium between cost and benefits. First, the cost of searching for a new mate is likely to be different. As mentioned above, time is a serious constraint when birds renest, and the time needed for mate assessment seems to be long (Sullivan 1994). Thus, searching for a new mate can result in the loss of breeding status or in a delay in the timing of breeding (Mills et al. 1996). There is abundant evidence that divorce between years delays the timing of breeding and is one of the main causes for a poorer breeding performance after divorce (e.g. Johnston & Ryder 1987). In Kittiwakes (*Rissa tridactyla*), the laying date may still be delayed even in the second year following divorce (Coulson 1966, Coulson & Thomas 1983). Probably, searching for a new mate after a first breeding failure delays breeding too long to allow a second clutch. Secondly, the probability of mate change depends highly on the availability of good quality mates (Ens et al. 1993). Birds will divorce when they have the chance to get a better quality mate. However, when birds renest most of the remaining birds are non-breeders or young breeders (Wendeln 1997) and the chances of obtaining a better quality mate are probably much lower than at the beginning of the breeding season. Thirdly, the cost of waiting for a mate that might not return at all is one of the factors that promote divorce between years (Coulson & Thomas 1980, Rowley 1983, Dhondt & Adriansen 1994, Gonzáles-Solís et al., in press). However, this cost is virtually negligable within a year as compared to between years, since the partner is already in the colony after the first breeding attempt.

Nest-site tenacity and mate retention

It has been suggested that the main factor that maintains the pair bond is site fidelity (Coulson & Thomas 1983, Cuthbert 1985). However, Fairweather & Coulson (1995) showed that when Kittiwakes prevented from nesting in the same nest-site between two consecutive years, pair bond was able to be re-formed in other

nest-sites or even other colonies. In our colony, some Common Terns changed their territory but not the mate when renesting, as observed by Massey & Fancher (1989) in the Least Tern (*Sterna antillarum*). This agrees with the hypothesis that mate fidelity does not arise solely from nest-site fidelity.

Acknowledgement

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