POPULATION DYNAMICS, RECRUITMENT, INDIVIDUAL QUALITY AND REPRODUCTIVE STRATEGIES IN COMMON TERNS *STERNA HIRUNDO* MARKED WITH TRANSPONDERS

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From 1992 to 1999, we used subcutaneously injected transponders, enabling remote and automatic annual identification with the aim of performing an integrated population study of a Common Tern *Sterna hirundo* colony. Within a few years, population parameters and their inter-year variation could be calculated with a high degree of accuracy (adult return rate 91%, subadult return rate 35%, breeding success 1.3 fledglings pair^{-1}y^{-1}, mean recruitment age 3y). Data on condition, fate, reproductive performance and output were gathered year by year and contributed greatly towards the detailed study of many questions in behavioural and population ecology, such as individuals' quality, prospecting and recruitment. The arrival time of prospectors and recruitment age were related to body condition. The high body mass of adults increased their reproductive performance and output. Divorce rate was low (18.9%) and increased with arrival asynchrony of mates. Divorced terns tended to change territories, whereas territory fidelity in general was high. The future focus of this ongoing study is reproductive value, senescence, lifetime reproductive success, fitness, and questions related to genealogy.

Key-words: *Sterna hirundo* - breeding - site fidelity - parental quality - timing - recruitment - arrival date - first breeding

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INTRODUCTION

Without the methodological instrument of ringing, studies of bird populations are impossible. Our knowledge of bird population dynamics is based mainly on long-term ringing. Recoveries are used to investigate mortality rates or dispersal, or populations are studied intensively and integratedly to gather knowledge of all relevant parameters pertaining to the dynamics and regulation of the population in question.

However, the use of ringing recoveries in population studies has a number of drawbacks, it requires extensive time series to gather the necessary data, and still requires many assumptions, estimations and models. Despite the frequently great efforts in well studied species some important demographic parameters are still poorly understood (e.g. Clobert & Lebreton 1991). Problems of disturbance through catching or of resighting probabilities, of man power or ring visibility and so on hamper effective ringing studies in long-lived species. In terns, for example, individual colour ringing has not proved successful: rings are rarely visible at any distance and are not durable, and extensive trapping and retrapping of ringed adults can cause clutch desertion, trap shyness, and unacceptable disturbance of the colonies
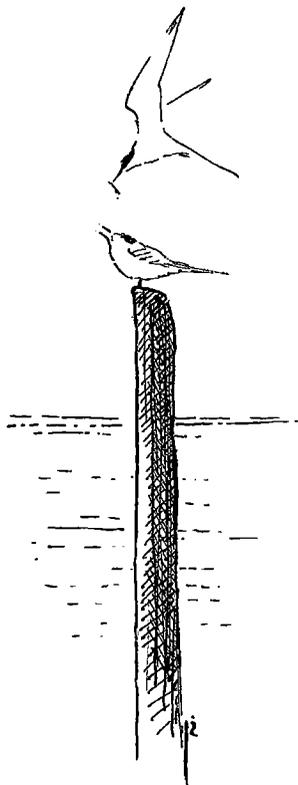
(Nisbet 1978; Kania 1992). Furthermore, the removal of steel rings by African people on the terns' wintering grounds poses a problem for population studies that use retrap or ring recovery analyses (Becker & Wendeln 1996; Wendeln & Becker 1999b).

To investigate long-term aspects of population ecology of the Common Tern, we developed methods of remote and automatic lifetime identification of individuals using passive transponders (Becker & Wendeln 1997), small injected microchips of unlimited lifespan. We started our studies in 1992 at a logistically favourable colony site. In this paper we present an interim overview of some results from the first years of the population study. By the methods used, within a few years important population parameters and their inter-annual variation can be derived with a high degree of accuracy to give insight into the mechanisms of population regulation. Furthermore, detailed data on the condition, fate, mating, reproductive performance and success of many individual birds are gathered year by year, thus providing material for the study of individuals' quality, lifetime reproductive success, fitness, prospecting and recruitment, as well as answers to genealogical questions.

METHODS

Field work was carried out from 1992 to 1999 in a Common Tern colony situated on six small artificial islands in Banter See in Wilhelmshaven (German North Sea coast). The islands (subcolonies) are rectangular, of equal size (10.7 x 4.6 m), and the distance between islands is around 0.9 m. During the course of the study, about 90-150 pairs per year bred in the colony site, except for 1997-99 when about 220-250 pairs bred. The population increase was due to immigration as well as to high breeding success over several years (Becker 1998 and below).

The studies are based on the technique of marking animals with transponders (microchips), which has been common practice since the end of

the 1980s and which permits the electronic identification of individuals without handling and disturbance (e.g. Elbin & Burger 1994). The implanted transponder provides an individual code of 10 alphanumeric characters. The microchip does not require a battery, has an unlimited lifespan and is activated and read by hand-held or stationary readers at a distance of ≤ 11 cm, regardless of light or environmental conditions. We use a small transponder (TROVAN ID 100, 11 x 2 mm), injected subcutaneously into the breast and permitting yearly identification without retrapping and handling. The details of marking and identifying the birds at the colony site remotely by an automatic antenna-system are presented in Becker & Wendeln (1997). The reading probability depends on the position of the transponder relative to the antenna. In our study, however, this is a minor problem, as birds visit nests and resting platforms frequently (see below) and most are in constant motion, thus increasing the probability of identification.

In 1992, we started tagging all fledged chicks of this colony allowing individual recognition throughout their life (1992-99: 1375 fledglings). From 1992-95, 101 adults were also marked. Since 1993, we have checked each nest every year in the colony for individuals bearing transponders by placing an antenna at the nest during the incubation period for 1-2 days. All islands are surrounded by a 60 cm high wall. The walls are provided with 42 locations for the terns to land and to rest (resting platforms). Antennas (12 1992-94; 22 1995-96; 30 1997-98; 35 1999) and balances (7-12) are regularly distributed among the platforms for identification and automatic recording of the terns' mass over the breeding season (for details see Wendeln & Becker 1996). In this way, both colony attendance and body mass of breeders and non-breeders are investigated, and our methods allowed detailed studies of the prospecting and recruitment processes.

Every year we marked each nest by a stake and its position was recorded once the breeding season was finished. For each breeding pair, laying date, egg size, laying order, the fate of the

eggs and chicks and their body mass growth were obtained from colony checks every two or three days during the breeding period. We measured the maximum length and breadth of the eggs to the nearest 0.1mm using Vernier callipers. The daily growth rate in the period of linear growth (3-13d) as well as maximum body mass of many chicks was determined. The age of many adults was known because they had been ringed as chicks in this colony since 1980. Adults were sexed by their courtship and copulation behaviour.

The investigations were performed under licences of the Niederächsisches Landesverwaltungsamt, Hannover, and of the Bezirksregierung Weser-Ems, Oldenburg (Nationalparkverwaltung; Tierschutzangelegenheiten).

Definitions and statistics

Body condition was recorded as the average mass of an individual bird for both the incubation and chick-rearing period (Wendeln & Becker 1999a). Similarly, we obtained body condition at the beginning of the season from the average of the mass records for each individual during their first day at the colony site, provided that this day was at least seven days before the laying date. The individual values of body mass, laying date and fledgling production are known to be consistent over years and to reflect individual quality in seabirds (e.g. Coulson & Porter 1985; Sydeman & Eddy 1995; Phillips & Furness 1998; Wendeln & Becker 1999a). We estimated the individual quality as the individual average values of these parameters over all years recorded, for those birds for which data from at least two years were available.

Population parameters were calculated using a simple population model (Henny 1972) assuming that subadults recruit into the colony and breed successfully when 4 years old, that emigration rates are low and that return rates of adult Common Terns correspond to survival rates. Subadult survival to age 4 is calculated by: subadult return rate x adult survival x 2. For further details see Wendeln & Becker (1998). Information on certain variables was lacking for some cases and there-

fore sample sizes vary somewhat between analyses. All tests are two-tailed and the level of significance was set to $P < 0.05$. Average values are presented as arithmetic means ± 1 SD except where otherwise indicated.

RESULTS

Population dynamics

During 1992-99 altogether 101 adult Common Terns and all 1375 fledged chicks of the colony have been marked with transponders. In 1998, we recorded 257 adults marked with transponders at the colony site in Banter See (177 breeders, including 78 recruits and 80 prospectors). From the cohorts 1992-95 (575 fledglings), 38% (218 individuals) had prospected and 22% (127) had recruited into the colony by 1998. These figures indicate the size of the database for various ecological investigations.

The breeding success was 1.3 fledglings pair^{-1} y^{-1} (1990-96). The return rates of adults ≥ 4 y of age and which had bred the year before ranged from 87 to 97% (mean 91%, 1999 included; Table 1). Until 1998, subadult return rate amounted to 35% (22-48%, five year classes 1992-96), and subadult survival to the age of 4 y was estimated to be at least 27% (cf. Wendeln & Becker 1998).

Table 1. Return rates of adult Common Terns of the Banter See colony 1993-99. Only birds ≥ 4 y old that have bred the year before are included.

Year	no. adults year before	no. adults returned	% returned
1993	33	29	88
1994	53	47	89
1995	70	61	87
1996	73	71	97
1997	75	68	91
1998	85	76	89
1999	120	111	93
average			91%

Table 2. Age-related proportion of non- breeders in the Common Tern colony Banter See. Data from 1992-98.

Age	% non-breeders	n
2	95	227
3	47	188
4	26	101
5	25	48
6	6	33
7-18	3	166

The average age of recruitment was 3 years. These values could account for an annual population increase of 8.5%, but population increase was in fact much greater in recent years. The observed population increase was most probably due to immigration from an adjacent colony (90 pairs in 1992 to 240 pairs in 1999; Becker 1998). Only 3% of adults were registered as non-breeders in some years ($\geq$ 7y old, n = 166; Table 2).

Prospecting and recruitment process

Most native prospectors first arrived at their colony at an age of 2y (86% 2y, 13% 3y; 2% $\geq$ 4y; n = 218), but did not usually breed (Table 2). Adult breeders arrived during April and early May, whereas prospectors arrived from June until August. The arrival date depended on age and experience (in 1997: 2y prospectors 24 June $\pm$ 9d, n = 80; 3y prospectors 17 June $\pm$ 23d, n = 9; 3y birds which had prospected the year before and therefore had some site experience 27 May $\pm$ 9d, n = 32; P < 0.001 compared with 2y prospectors, Tukey-test; compared with 3y prospectors without experience, n.s.). Most Common Terns recruited at an age of 3 years, during their second stay at the native colony site (Table 2). The age of recruitment seemed to depend on the year class and quality of the young (see below), and was relatively high in the 1992 cohort, leading to the relatively high value of 25% of 5y old birds not breeding until 1998.
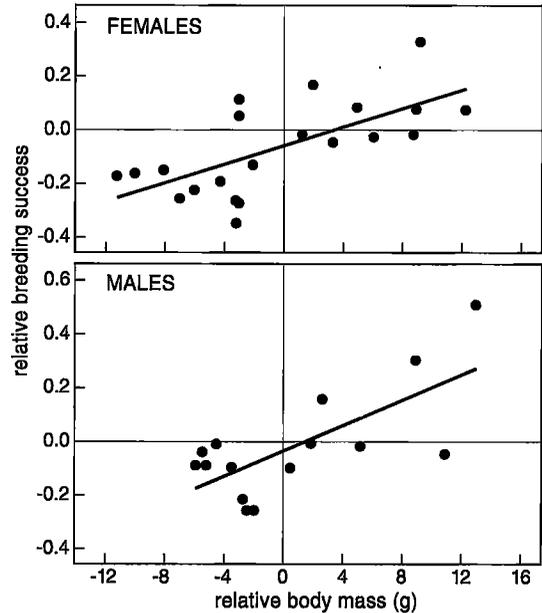

Fig. 1. The relationship between body mass and breeding success in Common Tern females (r_p = 0.67, n = 21, P < 0.005) and males (r_p = 0.70, n = 15, P < 0.005), relative to the annual colony average. Mean values of 2 - 5 reproductive seasons per individual (data from Wendeln & Becker 1999a).

Quality of adults

The reproductive fate of some individuals of the colony could be followed for many years. One example is a tern named 'Lotti' (ID 0026846C; Table 3). She was mated for 7 years with the same partner, 'Otto'. By the time she was ten years old in 1999, Lotti had produced 16 fledglings (average two fledglings per season), indicating the high quality of this bird. Reproductive performance improved with age. When five years old, in 1994, Lotti for the first time produced three fledglings. When six years old in 1995, highest values of egg mass, chick growth and body mass during incubation were achieved. This season was characterised by high food availability. At an age of seven, laying commenced earliest, on 8 May. In 1998 and 1999, when older than nine years, Lotti had the highest body mass during chick rearing, the most

Table 3. Breeding history of female 'Lotti', born 1989 (ID-Code 0026846C), nesting on island A. -: no data

Parameter	1992	1993	1994	1995	1996	1997	1998	1999
Partner	Jan	Otto	Otto	Otto	Otto	Otto	Otto	Otto
(ID-code)	0017A1F1	00F81D84	00F81D84	00F81D84	00F81D84	00F81D84	00F81D84	00F81D84
Laying date (May)	26	16	16	11	8	8	10	13
Egg mass (g)	17.3	18.7	19.3	20.7	18.3	19.0	19.0	17.7
Clutch size/ Brood size/ Fledglings	3/1/1	3/3/2	3/3/3	3/3/2	3/3/0	3/3/2	3/3/3	3/3/3
Growth rate of chicks (g d^{-1})	7.5	8.9	8.9	10.6	7.8	7.8	8.4	7.4
Body mass (g) during incubation and chick rearing	138/123	132/121	141/128	144/134	135/128	-/129	141/137	-/140
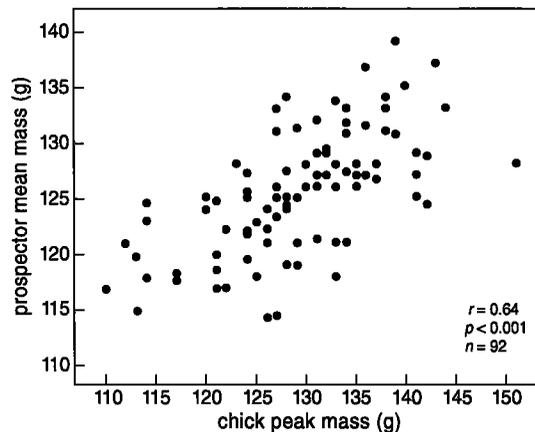
Fig. 2. Correlation of an individual's peak mass when a chick with its body mass in the year of first prospection at the natal colony in Common Terns from Banter See in Wilhelmshaven.

constraining period for adult Common Terns (Wendeln & Becker 1996), even if three chicks fledged successfully (average reproductive success 0.5 chicks pair^{-1} in 1998; 1.8 in 1999).

Not only in individuals but also in general the body mass of adult Common Terns showed high constancy over years (Table 3), and inter-individual differences reflect bird quality. The breeding success depended significantly on parental body mass (Fig. 1). High body mass was positively correlated with high breeding success, both in males and females. First data indicate that not only fledging success but also the prospecting rate of the young of an individual depended on its quality, measured as body mass (Becker 1999).

Quality of prospectors and recruits

Growth rate ($r = 0.27$, $n = 91$, $P < 0.01$) and even stronger peak chick mass (Fig. 2) of an individual were positively correlated with its mass when prospecting at the natal colony site. However, only small effects of body condition on return rates and on the probability to recruit were found (Becker 1999). In contrast, interesting relationships were detected between a fledglings peak mass, date of prospecting and age of first breeding (Fig. 3). The age of recruitment and chick peak mass were negatively correlated. Young recruiting at an age of three had higher peak mass as chicks than those that recruited at four years or older
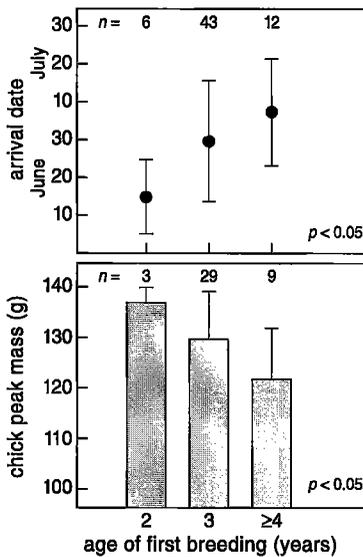
Fig. 3. Relationships of the age of recruitment of Common Terns and the date of first return to the natal colony as prospector (top; Kruskal-Wallis-test) and the peak mass during the chick period (bottom; Mann-Whitney U-test).

(Fig. 3). The latter also tended to have lower mass when prospecting. Young who commenced breeding at two years of age had highest peak mass (Fig. 3). Moreover, the age of recruitment was related to the date when a prospector arrived at the colony site for the first time. Birds recruiting at an older age had arrived as prospecting immatures on a later date (Fig. 3).

Divorce, mate and nest fidelity

Among 130 pairs in which both mates were individually marked, mate retention between years was 66.2%. Overall, the widow rate, as indicated by the proportion of pairs with one partner not returning to the colony the following year, was 18.5%. Among the 106 pairs in which both mates returned to the colony the next year, divorce rate was 18.9% (20 pairs).

A stepwise logistic regression analysis showed a significant effect of arrival asynchrony between mates to the breeding grounds on prob-
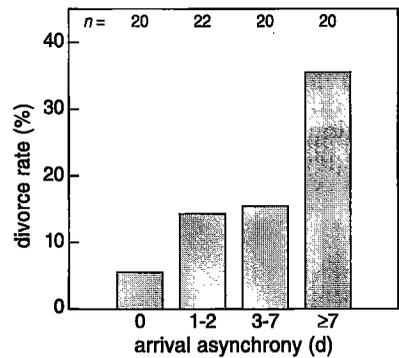

Fig. 4. Proportion of divorces depending on the number of days of asynchrony in arrival between mates. Numbers above bars show sample size.

ability of inter-season divorce ($\chi^2 = 12.96$, $df = 1$, $n = 82$, $P = 0.0003$, ß $= 0.151 \pm 0.051$ SE), whereas previous breeding success did not improve the model significantly. Median arrival asynchrony for divorced pairs was 7.5 d, whereas for reunited pairs it was 2 d, and all pairs with an arrival asynchrony greater than 16 d subsequently split up (Fig. 4). Among 20 divorced pairs, nine birds (22.5%) did not breed in the respective year, whereas among 24 widowed birds, only one (4.2%) did not breed. Difference in the rate of loss of breeding status between divorced and widowed birds was significant ($G = 4.5$, $df = 1$, $P < 0.05$). Of those birds that divorced, terns breeding with a new partner arrived at the breeding grounds significantly earlier (residual arrival date -0.8 $\pm$ 13.1 days, $n = 28$) than those birds that lost their breeding status in the season of their divorce (residual arrival date 17.4 $\pm$ 22.1 days, $n = 6$, Mann-Whitney U test $Z = -2.28$, $P < 0.05$). Divorced birds laid on average 7.0 days later and widowed 8.9 days later than reunited birds (Fig 5; ANOVA on log-transformed laying date to approach normality, males: $F_{2,88} = 7.27$, $P < 0.01$; females: $F_{2,97} = 14.40$, $P < 0.001$).

Faithful females changed subcolony significantly less (11%) than divorced (20%) or widowed females (50%, $n = 75$). To investigate nest site fidelity, the distance apart of nest sites
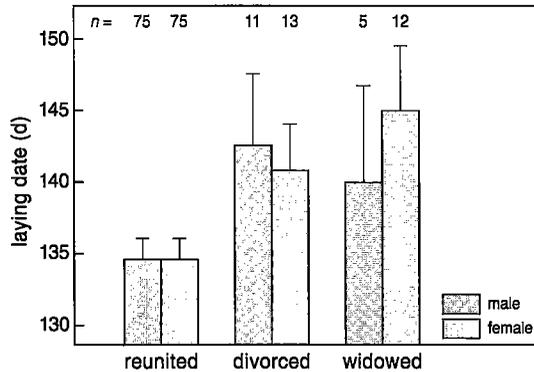
Fig. 5. Laying date (days from 1 January + CI 95%) in relation to the pair bond status for males and females. Numbers of each bar show sample size.

Fig. 6. Relationships between age (log-transformed) and laying date of birds that renested and those that did not renest. Birds with high probability of renesting (shaded area) are separated from birds with low renesting probability (unshaded area; $P = 0.5$).

between years was analysed. For 75% of 57 faithful pairs between two consecutive seasons, the distance moved was less than 1.25m. Nest site fidelity was high for faithful birds (mean ± SE in m, males 4.52 ± 1.37; females 4.52 ± 1.37), intermediate for divorced birds (for males, with 4.58 ± 4.53 we found a higher fidelity than for females 7.27 ± 4.21) and low for widowed birds (males 20.89 ± 9.82; females 13.17 ± 4.21; ANOVA on nest distances transformed logaritmically; males: $F = 3.92$, $df = 2,81$ $P < 0.05$; females: $F = 8.92$, $df = 2,91$ $P < 0.001$; LSD test for pairs of groups significantly different: faithful-widowed and divorced-widowed for males and faithful-widowed for females).

Renesting

After breeding failure, e.g. owing to predation by rats (eggs, chicks) or owls (chicks), the renesting probability was high in old birds that initiated their first clutch early in season (Fig. 6). Among 17 renesting pairs with both mates fitted with transponders, none showed intra-season divorce. For 75% of 26 pairs that renested within the same season, the nest site distance moved was less than 4.3m. Besides inter-year differences in mass of replacement eggs, egg mass was further affected by a seasonal trend. The later the first clutch was initiated ($r_p = -0.40$, $n = 35$, $P < 0.05$) or lost ($r_p =$
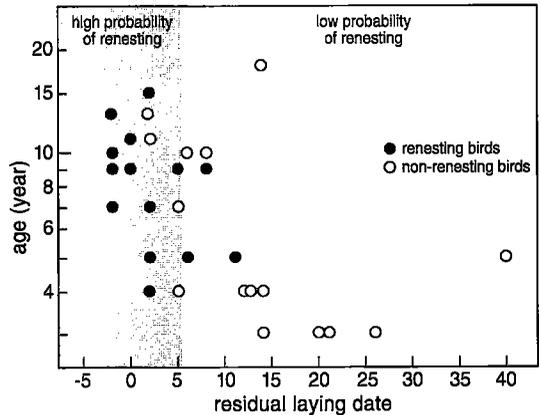
-0.46, $n = 35$, $P < 0.005$), the lower the mass of replacement eggs. A high mass of replacement eggs was produced by females that were mated with heavy males (high body mass during incubation before loss of first clutch; $r_p = 0.79$, $n = 10$, $P < 0.01$), stressing the importance of males for food provisioning to the female prior to egg laying. A reduced body mass of males in the second courtship period ($132 \pm 6g$; first period $136 \pm 5g$, $n = 12$; Wilcoxon-test: $P < 0.05$) and a higher mass increase of females prior to laying replacement eggs ($5.3 \pm 1.5g$ d^{-1}, prior to laying first eggs $3.9 \pm 1.7g$ d^{-1}; $n = 13$, Wilcoxon-test: $P < 0.05$) indicated that birds increased their effort in the second breeding attempt.

Genealogical studies

An overview was achieved not only of the number of fledglings of an adult or pair, but also of those young that later prospected and recruited the native colony. One individual example is once more female 'Lotti'. Of 10 of her chicks fledged by 1997, four had prospected the colony at age two, while three had recruited at age three by 1999. In 1997, daughter 'Lotta', born in 1994, fledged her first young and made 'Lotti' a grand-

mother. By 1999, Lotti had produced 16 fledg-lings and 9 fledged 'grandchicks'.

DISCUSSION

The method of marking birds with transponders overcame the problems associated with ringing in population studies of terns (see introduction) and enabled us to meet the requirements of a long term study of population ecology in this species.

Advantages

Tag implantation takes little time, and neither our observations of the behaviour, nor population parameters recorded indicate any negative effects on the birds (see also Elbin & Burger 1994; Nogge & Behlert 1990; Ball *et al* 1991; Schooley *et al* 1993; Wormuth 1991). Adult survival was high (Table 1; Wendeln & Becker 1998), and the number of fledged chicks per pair was independent of bearing a transponder (mates without transponders/one or both mates with transponder; 1997 0.9 chicks pair^{-1} ($n = 117$) / 0.9 ($n = 79$); 1998 0.4 ($n = 111$) / 0.5 ($n = 110$); Mann-Whitney's U-test, n.s.). A further advantage is the concealment of the transponder under the skin. Birds bearing rings or other external markers are more prone to being caught by people, and the markers are then likely to be removed. Among the two and three year old terns, we found at least 12 individuals bearing no steel ring which had presumably been removed by people in Africa (Wendeln & Becker 1999b).

With the use of transponders it is possible to identify wild birds of various body size and to record their occurrence, body mass or other parameters automatically and without handling them (Elbin & Burger 1994; Gendner *et al* 1992; Fraser & Trivelpiece 1994; Michard *et al* 1994). In this way, extensive and detailed data can be obtained. This has special advantages for long-lived smaller species like the terns in our study, in which ringing has not proved efficient for investigating demography. The logistically favourable site at Banter See allows registration of the complete colony (total population) and of the demographic parameters every year, resulting in average figures within a few years. Resighting probabilities are high, so that return rates are good estimators of survival probabilities (Cam *et al* 1998). Thus, integrated population monitoring and the study of the influences of environmental factors on population dynamics are possible.

Limitations

The small reading distance of the antennae limits the applicability to sites that are regularly used by individuals, such as resting or nesting sites and nesting holes. Sites must also permit the operation of electronic equipment in the field. For multi-annual data collection, species characterised by high site-fidelity meet these requirements. For reasons of practicability of the techniques, sites or colonies should be 'closed' and 'limited' to be able to check all marked birds using it. About one antenna per ten pairs should be available in order to ensure that all breeders can be checked, especially those of the laying peak. The transponder is relatively cheap, but the antenna system to identify the individual codes of the birds is expensive, limiting the applicability to special projects. Without antennae it is impossible to recognize if an individual is marked or not. Like rings, transponders may get lost, a problem we dealt with during the pilot phase of the present project (Becker & Wendeln 1997). For these reasons this marking method will not replace bird ringing, but it is a very useful tool in specific investigations in which it is much more effective than ringing.

The population data were collected within a few years and give precise annual figures of the return rates of adults, subadults and recruitment, since re-recording probabilities of the individuals at the colony site are very high. Population studies in birds based on ringing, however, in general need several decades of ringing huge numbers of birds every year. Even then the possibilities of studying inter-year variation in population parameters and their dynamic relationships are limited. Recruitment to our colony seems to be higher (> 22 %,

Wendeln & Becker 1998) than in the colonies studied in North America (6-14%, Nisbet 1978; DiCostanzo 1980). Our methods are especially well suited to the study of prospecting, which is so important in the recruitment of colonial birds (e.g. Danchin *et al* 1991, 1998). About 35% of the fledglings returned to their natal colony site, most of them by the age of two. As all fledglings of the colony are marked, the prospecting and recruitment of large numbers of individuals can be followed and investigated in detail. The first data achieved indicate the value of body condition for the recruitment process (cf. Kittiwake *Rissa tridactyla*, Porter & Coulson 1987; Porter 1988) as well as for the later quality of the breeders and for their reproductive output (Becker 1999; Wendeln & Becker 1999a). Next steps of investigations will be the study of possible differences in the rate or age of recruitment between male and female Common Terns, and the study of possible influences of the recruitment age and breeding success during the first years of reproduction on the survival of the young breeders. We plan also to check breeding Common Terns in adjacent colonies for emigrants from Banter See. Preliminary investigations suggest that emigration rates are low.

Individual reproductive histories from recruitment onwards (Table 3) can be derived from our data in large numbers in the course of the next few years. They allow the investigation of reproductive improvement with age, reproductive value, senescence, lifetime reproductive success and fitness (see below). The genealogical studies we perform will give insight into the individual's contribution to the next generation and to the colony, as well as the comparison of characteristics of parents and their offspring.

As in other seabirds (e.g. Wandering Albatross *Diomedea exulans*; Weimerskirch 1992), body mass in Common Terns determines breeding output in a given year (Wendeln & Becker 1999a). The long term identification and registration of individual body mass enables us to investigate changes in condition during a tern's life period and their effects on reproduction. After six years of our ongoing study, we found body mass to be a consistent parameter of bird quality (*cf.* Coulson & Porter 1985). The individual constancy of body mass is likely to lead to high repeatability of individual breeding performance and success, and we expect consequences for lifetime reproduction and fitness that may differ between individuals accordingly (Becker 1999).

Renesting after breeding failure renews the chance to raise young in a given season. Indeed, pairs producing a second clutch had a breeding success only insignificantly inferior to that of pairs with successful first clutches, but greater than that of pairs laying first but late (Wendeln *et al* 2000). The low relaying probability of late laying birds is probably an adaptation to the reduced chances of raising chicks later in the season (Parsons 1975; Becker 1996). Inter-year differences in mass of replacement eggs could be attributed to fluctuations in prey availability (cf. Safina *et al* 1988). Similarly, a seasonal decline in food availability could account for the seasonal trend in mass of replacement eggs (for further explanations see Moreno 1998).

Many aspects of behavioural ecology can be studied in birds marked with transponders, allowing remote and automatic identification. For example, nesting and mate fidelity can be addressed with particular accuracy (González-Solís *et al* 1998; 1999abc). Mate retention between two consecutive years was 66%, similar to other colonies (Austin 1947; Neubauer 1997). Inter-annual divorce rate was 18.9%, which is within the range reported for most gull species (from 10.5% to 30%, see review in Mills *et al* 1996). Results indicate that the main cause of divorce is the asynchrony between the arrival of mates at the breeding ground. Median arrival asynchrony for divorced pairs was 7.5 days whereas for reunited pairs was two days, and all pairs with an arrival asynchrony greater than 16 days subsequently split up. About 20% of divorced birds lost breeding status probably as a consequence of their late arrival. Consequences of divorce were restricted to the delay of seven days in the onset of laying. These results suggest that terns search for a new mate as soon as they arrive at the breeding grounds and

that mate fidelity is maintained so as to avoid the costs of searching for a new partner.

Most of the birds moved the nest-site within the colony either when renesting or between years, but dispersal distances did not differ significantly between and within years and were clearly shorter than would be expected from a random distribution of nests (González-Solís *et al* 1999c). Most of the new scrapes (> 75%) can be considered as lying within the previous territory, indicating a high fidelity to the territory, as found in other colonies (Austin 1949; Burger & Gochfeld 1991; Arnold *et al* 1998). Divorced and widowed birds, however, showed a lower fidelity to the previous territory. The deferred laying date for divorced and widowed birds probably favoured the pre-emption of their previous nesting sites.

ACKNOWLEDGEMENTS

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SAMENVATTING

Van 1992 tot 1999 werden onderhuids ingebrachte antwoordzenders gebruikt waardoor een geautomatiseerde individuele identificatie op afstand mogelijk werd van Visdiefjes *Sterna hirundo* in een kolonie in Duitsland. Het onderzoek maakte deel uit van een geïntegreerde populatiestudie van Visdiefjes en binnen enkele jaren konden enkele belangrijke demografische variabelen alsmede de verschillen tussen opeenvolgende jaren worden berekend met een exceptioneel grote nauwkeurigheid (terugkeer adulte vogels op de kolonie 91%, subadulte vogels 35%, broedsucces 1,3 uitgevlogen jongen paar^{-1}j^{-1}, gemiddelde leeftijd van eerste eigen broedsels 3j). Gegevens over de conditie en broedge-

drag en het daaraan gerelateerde broedsucces werden jaar na jaar verzameld en dit materiaal heeft enorm bijgedragen tot de oplossing van de talloze vraagstukken die samenhangen met de populatie-ecologie en het gedrag van deze sterns. Duidelijke verschillen in individuele kwaliteit van sterns konden worden aangetoond. De aankomstdatum van kolonieverkennende sterns en de leeftijd van eerste deelname aan het broeden waren beide gerelateerd aan de lichaamsconditie. Een hoog lichaamsgewicht van volwassen vogels was ook positief gerelateerd aan de kwaliteit als broedvogel en aan het aantal en de kwaliteit van uitvliegende jongen. Het uiteenvallen van broedpaartjes kwam weinig voor (18,9%) en nam toe naarmate partners een onderling sterker afwijkende aankomstdatum in de kolonie hadden. Sterns met nieuwe partners betrokken in de regel nieuwe territoria, terwijl bij gevestigde paren de plaatstrouw juist bijzonder hoog was. Toekomstig onderzoek zal zich toespitsen op de reproductieve kwaliteitsverschillen, seniliteit, reproductief succes gedurende het gehele leven, fitness en met genealogie samenhangende vragen. (CJC)