

S02-2 Individual quality and recruitment in the common tern, *Sterna hirundo*

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Abstract We investigated the individual histories of more than 1 300 fledglings from an intensively studied colony of common terns, *Sterna hirundo*. Based on six cohorts (1992–1998), which had recruited almost completely by 2002, we found that the body mass of a fledgling was positively related to return and recruitment probability. Even in subadult stages, pre-fledging characteristics affect the probability of recruitment in this medium-sized seabird. Our results tend to be consistent for both sexes. In addition, older age at fledging reduced recruitment probability, particularly for late fledged young, reflecting indirectly on parental quality. However, other parameters of the egg and nestling period, such as clutch size, hatching order, and number of fledglings per brood, had no influence on recruitment of fledged young. The results suggest that body mass of young can be used as a predictor of recruitment probability and as an indicator of individual quality. These conclusions are discussed in the light of the meager information on pre-fledging characteristics and post-fledging survival in birds.

Key words Fledging mass, Pre-fledging characteristics, Post-fledging survival, Natural selection, Philopatry

1 Introduction

Only a small percentage of fledged young are recruited into the breeding populations of birds (review in Newton, 1989). In the common tern (*Sterna hirundo*), for example, barely a quarter return (Becker et al., 2001). Obviously, strong selection pressures operate during the pre-breeding stage. Effects of pre-fledging characteristics for survival in the natal period are well known and described for different seabirds (e.g., Parsons et al., 1976; Viksne and Janaus, 1990; Spear and Nur, 1994; Nisbet et al., 1995; Royal and Hamer 1998). Although some investigations have been able to show an influence of these parameters on survival after fledging, other studies have found none (Table 3). Accordingly, we ask here: do parameters of individual "quality" such as body mass, which is constant across years in individual terns (Becker and Wendeln, 1999), and other pre-fledging characteristics, influence return and recruitment of individual common terns in natal colonies?

2 Materials and methods

Our studies were carried out over 1992–2002 at the common tern colony "Banter See" in the harbor of Wilhelmshaven on the German North Sea coast (Becker et al., 2001). Over that period the colony increased from 90 to 280 pairs. All nests were marked and checked every 2–3 days to record the fate of eggs and banded chicks. Most chicks were also weighed to obtain continuous data on growth until fledging. All fledglings were marked with transponders enabling annual and lifetime identification (Becker and Wendeln, 1997).

Year after year, marked breeders as well as non-breeders were recorded remotely and automatically by an antenna system (Becker and Wendeln, 1997; Ludwigs and Becker, 2002), in order, according to the total population approach, to detect all returning and prospecting individuals as well as natal recruits. Any bird not re-recorded in the natal colony was

Table 1 Survival of common tern fledglings until recruitment in relation to different pre-fledging characteristics

Characteristic	B ± SE	Wald	df	P
Hatching order	-0.029 ± 0.151	0.036	1	0.849
Fledglings per brood	0.130 ± 0.150	0.752	1	0.386
Fledging date	-0.002 ± 0.009	0.029	1	0.866
Fledging age	-0.010 ± 0.036	0.081	1	0.776
Fledging mass	0.027 ± 0.012	5.537	1	0.019

Cohorts 1992–1998, multiple logistic regression, dependent variable = recruited or not until 2002: -2 log likelihood = 597.97, $\chi^2 = 7.64$, $df = 5$, $P = 0.177$, $n = 469$.

Table 2 Influence of fledglings per brood on recruitment rate in common terns

Fledglings per brood	Fate of the fledged tern					
	Not returned		Returned only		Returned and recruited	
One	130	54.9%	37	15.6 %	70	29.5%
Two	219	59.3%	41	11.1 %	109	29.5%
Three	101	56.1%	21	11.7 %	58	32.2%

Cohorts 1992–1998 ($\chi^2 = 3.375$; $df = 4$; $P = 0.497$)

considered as dead. We sexed terns by their mating behavior at the colony site. Beginning comprehensively in 1998, we sexed all fledglings by PCR, maintaining that information for all fledglings including non-returners.

From these data we analyzed the influences of pre-fledging characteristics on return and recruitment in the natal colony. The analyses cover all fledglings of cohorts 1992–1998 and their fate (= recruited or not) until 2002. Because the majority (~90%) of all fledglings were recruited to the natal colony within four years (Ludwigs and Becker, 2002), we include here nearly all recruits out of the total 983 fledglings from the seven cohorts, except for a few birds still to be recruited in ensuing seasons. In some cases, information on some variables was missing; and sample sizes therefore vary between analyses: χ^2 -test, T -test, ANOVA. In the logistic regression (Table 1), we did not use all pre-fledging characteristics measured, in order to prevent proliferation of subgroups with small sample sizes. The level of significance used in the analyses is $P < 0.05$.

3 Results

41% of fledged cohorts 1992 through 1998 returned as prospectors from 1994 through 2002, and 28% were recruited into their natal colony at Banter See. During the subadult period, most pre-fledging characteristics had no influence on recruitment of the fledglings, which had left the colony (Table 1).

3.1 Clutch and nestling characteristics

Clutch size had no influence on recruitment (two and three eggs only: $\chi^2=0.558$; $df=2$; $P=0.756$; $n=834$). Neither did hatching order ($\chi^2=1.646$; $df=4$; $P=0.800$; $n=677$) nor the number of fledglings per brood (Table 2), or even on return to the colony (Table 1).

3.2 Fledgling characteristics

Body mass of fledglings was very significantly different between recruits and terns not recruited. On average, the body mass of fledglings recruited was 2% higher than those not (maximum chick mass: 127.8 ± 9.2 g versus 125.5 ± 9.4 g, $T_{582} = 2.766$, $P < 0.01$; fledging mass: 119.3 ± 8.6 g versus 117.2 ± 9.5 g, $T_{582} = 2.488$, $P < 0.02$). Both mass parameters were related to return and recruitment probability, but in this paper we concentrate on fledging mass (Fig. 1, Table 1). Even in the broader group of returned fledglings, this parameter affected the chance of recruitment into the colony according to the analysis: returned terns of the cohorts

1992–1998; dependent variable: recruited or not until 2002; log.reg.: $B = 0.032 \pm 0.016$; Wald = 4.126, $df=1$, $P < 0.05$, $n = 256$. Of the fledglings recruited into the colony, 10%–35% reflected the effect of fledging mass (Fig. 1).

Both fledging age and fledging date were correlated negatively with fledging mass, but fledging age was correlated positively with fledging date. What this means is that old fledglings left the colony late in the season. However, a partial correlation of mass with fledging age corrected for fledging date revealed the importance of fledging age rather than date for recruitment (fledging age by fledging mass controlled for fledging date: $r = -0.280$; $P < 0.001$). Terns fledged older were lower in mass. The fledging mass of birds with median fledging age (25–27 d; 118.6 ± 7.9 g) was similar to the mass of those fledged younger (119.8 ± 8.6 g), but both groups differed significantly from terns fledged older than 27 d (114.1 ± 11.5 g; ANOVA: $F_{2,580} = 16.528$, $P < 0.001$; post hoc Scheffé-test result: fledglings <25 d and 25–27 d versus >27 d; $P < 0.001$).

The difference of fledging mass between recruits and non-recruits was particularly distinct in the old fledged young (>27 d; 116.6 ± 9.5 g versus 113.2 ± 12.0 g; T -test: $T_{134} = 1.487$, $P = 0.139$). When cohort 1999 (not yet completely recruited by 2002) was included, this difference became significant: 116.5 ± 9.8 g versus 111.5 ± 11.6 g; T -test: $T_{190} = 2.464$, $P < 0.02$. From another view, recruited late fledged young (>2 d later than the median date) were significantly younger at fledging than those not recruited (26.5 ± 2.9 d versus 27.8 ± 3.6 d; T -test: $T_{335} = -2.867$, $P < 0.005$); but this was not found in terns that fledged early or at median dates (T -test, n.s.).

3.3 Sex differences in fledging mass and recruiting rates

There were some differences between females and males in recruiting rates and fledging mass (Fig. 2), with fledging mass showing a tendency to influence recruitment in both (Fig. 2; combined data: $B = 0.029 \pm 0.012$; Wald = 5.893, $df = 1$, $P < 0.02$).

3.4 Fledging mass and recruitment age

We found no effect of fledging mass on age of recruitment. The mean fledging mass of 3-year-old recruits (118.1 ± 8.0 g) was similar to younger (118.1 ± 8.4 g) or older recruits (119.7 ± 9.6 g; ANOVA: $F_{2,220} = 0.769$, $P = 0.465$). A separate analysis for each sex indicated no significant effect either. According to the data for males: cohorts recruited completely 1992–1997; $n=77$; 2 year old = 120.0 (3.6 g, 3 y = 120.2 ± 6.9 g, >3 y = 121.5 ± 9.6 g). However, in females, a nega-

Table 3 Studies reporting effects of pre-fledging characteristics on post-fledging survival in long-lived birds

Characteristic	Influence	No influence
Clutch size	15, 18	22
Hatching order	18	8, 15, 22
Hatching date*	5–7, 9, 10, 13–17	2, 4, 12, 21
Fledgl. per brood	15	22
Growth rate	18	
Body size	1	
Chick peak mass	6, 22	21
Fledging mass	2–6, 22	(12), 19, 21
Body condition	1, 11, 13	19
Fledging age	22	12, 21

*or fledging date

1. *Diomedea exulans* (Weimerskirch et al., 2000).
2. *Calonectris diomedea* (Mougin et al., 2000).
3. *Puffinus gravis* (Elliot et al., 1973).
4. *Puffinus griseus* (Richdale, 1954; Sagar and Horning, 1998).
5. *Puffinus puffinus* (Perrins 1966; Perrins et al., 1973).
6. *Sula capensis* (Jarvis, 1974).
7. *Phalacrocorax aristotelis* (Harris et al., 1994).
8. *Egretta garzetta* (Hafner et al., 1998).
9. *Anser caerulescens* (Cooke et al., 1984).
10. *Aythya affinis* (Dawson and Clark, 2000).
11. *Somateria mollissima* (Christensen, 1999).
12. *Haematopus ostralegus* (Kersten and Brenninkmeijer, 1995).
13. *Stercorarius parasiticus* (Phillips and Furness, 1998).
14. *Catharacta skua* (Catty et al., 1998).
15. *Larus ridibundus* (Viksne and Janaus, 1993).
16. *Larus argentatus* (Nisbet and Drury, 1972; Parsons et al., 1976).
17. *Larus occidentalis* (Spear and Nur, 1994).
18. *Rissa tridactyla* (Coulson and Porter, 1985).
19. *Uria aalge* (Hedgren, 1981, Harris et al., 1992).
20. *Alca torda* (Lloyd, 1979).
21. *Fratercula arctica* (Harris and Rothery, 1985).
22. *Sterna hirundo* (this study).

tive trend in fledging mass with recruitment age was suggested: $n = 61$; $2y = 122.0 \pm 6.1$ g, $3y = 118.6 \pm 8.2$ g, $>3y = 117.3 \pm 11.6$ g, ANOVA n.s.).

4 Discussion

There are very few studies addressing influences of pre-fledging characteristics on post-fledging survival in long-lived birds, particularly with respect to body mass. Moreover, all such investigations listed in Table 3 are based on ring recoveries, resightings and/or live recaptures, where the effort spent on recatching or resighting particular banded birds carries limitations. Consequently, the proportion of recovered to unrecovered birds can be very low, often $<3\%$ versus $>97\%$ and almost never as high as 10% versus 90% (e.g., Hedgren, 1981; Viksne and Janaus, 1993; Phillips and Furness, 1998). Therefore it seems likely that such studies include moderate proportions of surviving birds in their groups of non-returners, as some workers have admitted: about 10% estimated by Harris and Rothery (1985). Recorded differences in proportions of surviving versus lost individuals are thus biased against survivors, particularly

where the differences are small or, as Nisbet (1996) points out, the data are “relatively insensitive to detect influences”. The use of transponders in our common tern study enabled us to use a total population approach by recording each individual returning to the natal colony ($>40\%$ of fledglings). However, dispersal rate could not be calculated.

Nearly all pre-fledging characteristics investigated here were unimportant for post-fledging survival in common terns (also Dittmann et al., 2001). Body mass, however, is a decisive pre-fledging factor for recruitment. Even if the difference in pre-fledging mass was only a few grams (2% of body mass), it had a significant influence on recruitment probability. In some shearwaters and the South African gannet (*Sula capensis*), several studies have also shown the importance of high fledging mass for post-fledging survival (Elliot, 1970; Jarvis, 1974) or for return to the natal colony (Perrins et al., 1973; Sagar and Horning, 1998), or survival until breeding age (Mougin et al., 2000). Shearwaters have to manage the time after fledging without adult guidance. In consequence, mortality is high immediately after fledging and fledglings need to leave their colony as fat as possible (Mougin et al., 2000), as reflected in distinct mass-differences between returners and non-returners, small sample sizes notwithstanding.

Terns benefit from prolonged parental guidance after fledging (Burger, 1980; pers. obs.). In this respect, they could be described as intermediate between auks, which leave the colony under parental care at a pre-fledging stage (Lloyd, 1979; Hedgren, 1981; Harris et al., 1992), and shearwaters, which are all but independent at fledging (Perrins et al., 1973; Sagar and Horning, 1998; Mougin et al., 2000). Chicks of common murre (*Uria aalge*) (Hedgren, 1981; Harris et al., 1992) and razorbills (*Alca torda*) (Lloyd, 1979) leave the colony long before independence, and are fed by their parents for a long period at sea before reaching their “independence” mass. That may well be one reason why, in the Alcidae, no evidence has been found for any influence by pre-fledging body mass on survival after fledging.

Our results for the effect of fledging body mass on survival support those from other species in which parental care is reduced or lacking at the post-fledging stage. Similar pre-fledging characteristics, such as body size in male wandering albatrosses (*Diomedea exulans*) (Weimerskirch et al., 2000), body condition in arctic skuas (*Stercorarius parasiticus*), common eider females (*Somateria mollissima*) and wandering albatross females (Phillips and Furness, 1998; Christensen, 1999; Weimerskirch et al., 2000), and growth rates in kittiwakes (*Rissa tridactyla*) (Coulson and Porter, 1985), and their positive correlation with survival after fledging, support the generality that individual body mass at early stages of life is significant for later recruitment probability in long-lived birds, just as it is in songbirds (e.g., Garnett, 1981; Magrath, 1991; Ringsby et al., 1998; Both et al., 1999; Naef-Daenzer et al., 2001).

As Sagar and Horning (1998) suggested for shearwaters, sex-related philopatry which is higher in males,

and the tendency of males to be larger than females, might influence mass-related survival in fledglings. In the common tern, the sexes showed differences in philopatry and mass dimorphism (Fig. 2). Both sexes, nevertheless, trended in the same way, so we consider that our results were not mediated by sex-related differences.

Hatching date has an influence on post-fledging survival in a number of species (Table 3). Most workers have not clearly separated the periods before and after fledging in their studies, because chicks were often banded and measured at some time during development, without knowledge of whether they actually fledged. As a parameter for survival, hatching date is much easier to use than age at fledging age or body mass during development which need more effort in fieldwork.

In the common tern, fledging age and not hatching or fledging date was a principal factor affecting recruitment probability. The advantages of hatching or fledging early are described in the literature as direct effects influencing survival, as in providing more time to prepare for migration (Cooke et al., 1984; Dawson and Clark, 2000), establishing dominance over late-fledged young (Nisbet and Drury, 1972; Spear and Nur, 1994), and allowing more time to gain experience in hunting (Newton, 1986), or indirect effects, such as parental quality (Spear and Nur, 1994; Catry et al., 1998). In late fledged common terns, we found lower masses, particularly in terns fledged >2 d later than the median fledging date. These older and lighter fledglings were handicapped.

Fledging age rather than date suggests here an indirect effect: reduced parental quality in parents that breed late and need more time to rear their young. In comparison, high quality breeders are those that can rear their young and bring them to high mass levels in a shorter time, even late in the season. In the snow petrel (*Pagodroma nivea*), Tveraa and Christensen (2002) found evidence that fledging mass of young is affected by parental quality, because

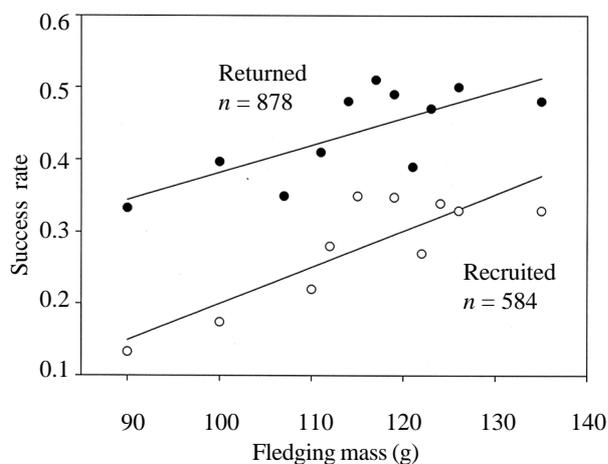


Fig. 1 Return and recruiting rate of common terns in relation to fledging mass

Fledging mass showed a significant influence on return rate (cohorts 1992–1999 log. reg. = $B = 0.019 \pm 0.007$; Wald = 6.617, $df = 1$, $P < 0.02$) and recruiting rate (cohorts 1992–1998 log. reg. = $B = 0.025 \pm 0.010$; Wald = 6.069, $df = 1$, $P < 0.02$).

adults with higher body condition guarded their chicks for a longer periods and left them with higher body mass at independence. In the thick-billed murre (*Uria lomvia*), Hipfner (2001) found no differences in survival to recruitment age between early- and late-hatched chicks if late-hatched young came from replacement clutches. Thus, the influence of hatching date advocated in such studies might reflect other pre-fledging characteristics instead, notably body mass and the indirect effect of parental quality.

The positive link between fledging mass and recruitment probability in the common tern was evident at different stages of subadult life, at first return to the natal colony when two or three years old (Fig. 1), and during the prospecting period until recruitment at least one year later (Ludwigs and Becker, 2002). In Kittiwakes, recruits showed higher body masses in their year of first breeding compared to prospectors of the same year (Porter and Coulson, 1987), indicating the immediate importance of body mass in the decision to breed. However, we found no mass differences between recruits of different age in the common tern. Owing to sexual differences in the mass of fledglings, and the younger recruitment age of female common terns (Ludwigs and Becker, 2002), it was necessary to separate sexes; females recruited younger tended to be heavier. For males, other factors seem to influence delayed first attempts to breed.

Body mass has been found to be an important parameter for survival not only for the subadult period but also in other aspects of life history in the common tern. It is positively linked with reproductive success (Wendeln and Becker, 1999), related to fitness (Becker, 1999) and seems to be highly heritable (unpubl. data), as Phillips and Furness (1998) suggested for body condition in the arctic skua. The evidence presented here for the decisive influence of pre-fledging and fledging body mass on survival and recruitment in the common tern leads to the assumption that this phenomenon may be more widespread in birds than supposed so far.

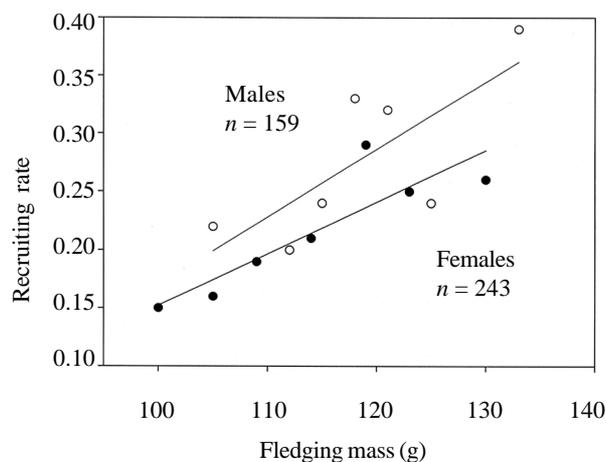


Fig. 2 Recruiting rate of common tern in relation to sex and fledging mass

Cohorts 1997–1999, dependent variable — recruited or not until 2002: females log. reg., $B = 0.020 \pm 0.017$; Wald = 1.319, $df = 1$, $P = 0.251$; males log. reg., $B = 0.030 \pm 0.020$; Wald = 2.235, $df = 1$, $P = 0.135$.

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