

Post-fledging body mass as a determinant of subadult survival in Common Terns *Sterna hirundo*

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Abstract Once a bird has fledged it becomes hardly accessible for researchers and consequently knowledge about post-fledging ontogeny is scarce. In this study on juvenile Common Terns (*Sterna hirundo*) we used an automated transponder-based detection and weighing system at Banter See colony, Northern Germany, which enabled us to investigate body mass growth of post-fledglings and its consequences for their survival until first return to the natal colony when 2 years old. We analysed data from two contrasting breeding seasons, 2000 and 2001, in order to determine inter-year and inter-sex variation of post-fledging parameters assumed to potentially affect subadult survival, such as the period a juvenile is still present at colony surroundings (departure age), its fledging mass and last recorded post-fledging body mass, and hatch date. Using an information-theoretic model selection approach, neither the date of hatching nor the departure age was found to affect survival. The only predictor of survival was last post-fledging body mass whereas fledging mass itself was of minor importance. Although there was weak evidence for an interaction with year, individuals of the cohort 2000, which left the colony area on average 5 g lighter than those reared under the more favourable conditions in 2001, did not exhibit lower return probability. We suggest that under unfavourable conditions selection had eliminated weak individuals prior to fledging or during the post-fledging period. This study underlines the importance of the post-fledging period and its consequences for

survival, especially in species with prolonged parental care post-fledging.

Keywords Post-fledging body mass · Post-fledging survival · Hatch date · Subadult return · Departure age

Introduction

The post-fledging period is a critical stage during the transition to independence, and therefore it can have major consequences for survival of young birds (review by Starck and Ricklefs 1998). However, knowledge about mechanisms involved in post-fledging development is limited, mostly due to methodological restrictions. Therefore, pre-fledging characteristics are often used to predict the survival of offspring because they are relatively easy to monitor.

In seabirds, information on factors influencing subadult survival has been obtained by many studies on procellariids (Perrins et al. 1973), sulids (Jarvis 1974), larids (Parsons et al. 1976; Coulson and Porter 1985; Spear and Nur 1994; Nisbet 1996; Cam et al. 2003), and alcids (Hedgren 1981; Harris and Rothery 1985; Harris et al. 1992, 2007). In each group, post-fledging survival was affected significantly by one or more aspects of the pre-fledging period including brood size, hatching order, hatching date, and fledging weight. In the Common Tern (*Sterna hirundo*), previous studies did not find an effect of brood size or hatching order on post-fledging survival (Nisbet 1996; Dittmann et al. 2001). Schaubroth and Becker (2008) reported no significant relationships between fledging mass and post-fledging survival probability during the first weeks after fledging, which was consistent with studies conducted on Sandwich

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Terns (*Sterna sandvicensis*) (Stienen and Brenninkmeijer 2002) and Sooty Terns (*Sterna fuscata*) (Feare 2002). Stienen and Brenninkmeijer (2002) suggested that low fledging mass might be overcome by continued parental provisioning after fledging, as Sandwich Tern fledglings accompany their parents to the foraging areas, thereby reducing the risk of kleptoparasitism. Accordingly, Common Tern fledglings benefit from prolonged parental care during transition to independence (Burger 1980), resulting in a continuous mass increase after fledging in preparation for migration (Schauroth and Becker 2008). The proximate consequences of post-fledging mass growth on survival until return to the natal colony and the question which other post-fledging characteristics may play a role in predicting the likelihood of survival are the focus of this paper.

A transponder-based detection system at Banter See colony in Northern Germany, which includes automatic balances, enabled us to investigate this frequently neglected period and its consequences for first return to the natal colony. In a previous study at this colony site, Schauroth and Becker (2008) found that the degree of mass increase is associated with the prevailing environmental conditions: in 2001, a year with favourable conditions resulting in an above-average reproductive success (1.8 fledglings per pair), post-fledglings generally reached higher body mass than in the poor year 2000 (0.8 fledglings per pair and high post-fledging mortality), even though full adult body mass was not attained. Likewise, sexual differences in body size were more pronounced when environmental conditions were favourable (Schauroth and Becker 2008). Consequently, it seems likely that these two cohorts exhibit inter-year and inter-sex variation in survival rates. In order to test this hypothesis, we used data on the same individuals as Schauroth and Becker (2008) and completed the dataset by including information on their return status. The further aim of this study was to determine whether post-fledging characteristics can be used to predict subadult survival probability.

Methods

Study site and data collection

The study was conducted at the Common Tern colony situated in the harbour area of Wilhelmshaven, Lower Saxony, Germany (53°30'40"N, 8°06'20"E) during two consecutive breeding seasons 2000 (235 breeding pairs) and 2001 (250 breeding pairs). The colony site consists of six artificial islands each 10.7 × 4.6 m arranged in a line 0.9 m apart. The islands are surrounded by concrete walls (60 cm high) equipped with a total of 44 elevated platforms for the terns to land and rest on. All fledglings have been

ringed and marked with subcutaneously injected unique transponders (TROVAN ID 100), which could be read by an antennae (record interval 5–10 s) installed at each of the 44 resting boxes. About 16 of the boxes were equipped with electronic balances (DIGI 2000, accuracy ± 1 g). This system recorded individual transponder codes and weights of all marked birds, including post-fledglings resting on the platforms prior to departure from the colony. Further details of this automatic detection system, which minimises anthropogenic interference by preventing the need for trapping, are presented in Becker and Wendeln (1997) and Becker et al. (2008). Apart from this, all nests and chicks were checked at 2- to 3-day intervals and most chicks were weighed continuously until fledging (digital balance, accuracy ± 1 g; details in Wagener 1998). Chicks were sexed using molecular methods (Kahn et al. 1998).

Terms and definitions

Sex and year were identified as two categorical variables potentially important in the processes measured. The study encompassed only two, but contrasting, years and thus year serves as a two level factor (2000 = 'poor', 2001 = 'good') and we expected to find effects of year interacting with covariate measures of timing and growth. Sex might also interact with covariates as previous studies have shown that sex-specific differences in body mass were more pronounced when conditions were favourable (e.g. Becker and Wink 2003; Schauroth and Becker 2008). The following covariates were measured for each surviving individual (fledgling not recorded as dead until departure in the same season), and justifications and definitions are listed below (see Fig. 1 for an overview):

- **Hatch date (HD):** considered a surrogate measure of parental quality as early breeders show higher reproductive performance (Arnold et al. 2004). HD was defined as the day (day of year) a chick was found for

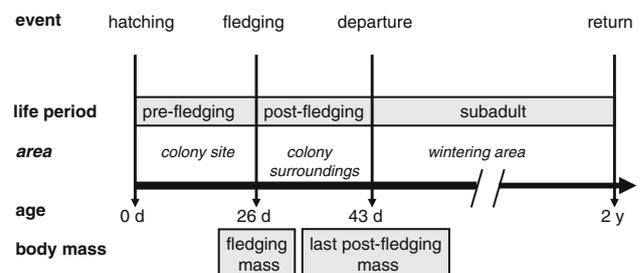


Fig. 1 Early life stages of a Common Tern (*Sterna hirundo*) and term definitions. See “Methods” for parameter descriptions. Mean fledging age 26.2 days ($n = 239$; 2000: 28.0, 2001: 25.6). Mean departure age 43.0 days ($n = 239$; 2000: 48.7, 2001: 40.4). Note: although the majority of subadult Common Terns returns at the age of 2 years, the dataset also contains individuals returned >2 years

the first time if it was freshly hatched, otherwise the previous day was designated as date of hatching

- *Departure age (DA)*: the total time a juvenile is present at the colony computed as period from hatch date until last post-fledging record, the last day (day of year) when a juvenile was registered at the colony surroundings. The post-fledging time between fledging and last record of a young differed between years (range 2000: 2–49 days, mean ± SD = 20.7 ± 12.0, n = 81; range 2001: 1–58 days, mean ± SD = 14.8 ± 12.8, n = 158; Schaubroth and Becker 2008)
- *Fledging mass (FM)*: the last recorded mass (g) of a chick prior to fledging
- *Last post-fledging mass (LPFM)*: the last recorded mass (g) in the season, which is indicative of the bird’s condition before leaving the colony area (Schaubroth and Becker 2008); it is correlated with ‘mean post-fledging mass’ (r = 0.894, P < 0.01, n = 239) and fledging mass (r = 0.211, P < 0.01, n = 239)
- *Survival to return*: local return rate of post-fledglings to their natal colony, almost always when 2 years old, to prospect the colony (Dittmann and Becker 2003)

Since not all juveniles of a cohort could be registered after fledging, we need to control for differences between the two groups of registered and not-registered birds. Therefore, Schaubroth and Becker (2008) compared fledging mass and fledging age of both groups and did not find any significant variation in relation to colony attendance. We also checked whether both groups differed in terms of

return rates and did not find significant variation ($\chi^2 = 0.868, P = 0.352$).

Data analysis and statistics

We used χ^2 statistics to test for annual variation in return rates. Pearson correlation coefficients were used to test relationships between parameters. MANOVA and GLM were used to determine the effect of year, sex and their interaction on the dependent continuous variables last post-fledging mass, hatch date, and departure age (Table 1) irrespective of their return status. If not otherwise stated, we present means with standard deviation (±SD). All tests were two-tailed, and the level of significance was $P \leq 0.05$.

In order to analyse the simultaneous effects of categorical (year, sex) and continuous (e.g. last post-fledging mass, hatch date, departure age) explanatory variables on the binary response variable (returned: yes/no), we used ANCOVA models with a binomial error structure and the logit link function. We generated an a priori set of candidate models that we considered to have reasonable biological support and used an information-theoretic approach to compare support among competing models (Burnham and Anderson 2002). This approach has recently received increasing attention as a useful tool for model selection in ecological studies. In contrast to classic null hypothesis tests, model selection criteria can be used to rank competing models, to weigh the relative support for

Table 1 Post-fledging characteristics of Common Tern (*Sterna hirundo*) fledglings in 2000 and 2001

Covariate	Year	Sex	Mean ^a	Returned	Not returned
Last post-fledging mass (g)	2000	Male	121.4 ± 14.4 (38) ^b	121.5 ± 8.8 (20)	121.3 ± 19.1 (18)
		Female	118.3 ± 10.7 (40)	118.8 ± 10.0 (15)	117.9 ± 11.2 (25)
	2001	Male	127.6 ± 12.3 (70) ^{b,c}	130.4 ± 13.4 (34)	124.9 ± 10.7 (36)
		Female	121.5 ± 11.3 (88) ^c	124.1 ± 10.0 (37)	119.5 ± 11.9 (51)
Hatch date (day of year)	2000	Male	154.8 ± 5.8 (38) ^b	154.2 ± 4.2 (20)	155.4 ± 7.4 (18)
		Female	153.9 ± 4.9 (40) ^b	153.2 ± 4.0 (15)	154.3 ± 5.5 (25)
	2001	Male	163.0 ± 14.0 (70) ^b	162.3 ± 11.7 (34)	163.7 ± 16.1 (36)
		Female	167.0 ± 15.8 (88) ^b	165.8 ± 13.5 (37)	167.8 ± 17.4 (51)
Departure age (day)	2000	Male	46.5 ± 10.7 (38)	44.4 ± 9.4 (20)	48.7 ± 11.8 (18)
		Female	50.6 ± 13.1 (40) ^b	50.7 ± 11.5 (15)	50.6 ± 14.2 (25)
	2001	Male	42.2 ± 14.1 (70)	42.9 ± 14.2 (34)	41.6 ± 14.2 (36)
		Female	38.7 ± 12.5 (88) ^b	40.0 ± 12.1 (37)	37.8 ± 12.8 (51)

Mean ± SD, n in parenthesis. Means from Schaubroth and Becker (2008). Besides the mean, the values are separated between returned and non-returned individuals

^a The influence of year, sex, and their interaction was tested by MANOVA (see text for details). All juveniles surviving the post-fledging stage were included in the analysis, irrespective of return state. Year: $F_{3,230} = 21.278, P < 0.001$; sex: $F_{3,230} = 3.587, P = 0.014$; interaction year × sex: NS

Pairs of rows sharing the same letters denote significance ($P < 0.05$); ^binter-year differences if GLM had shown a significant effect; ^cinter-sex differences if GLM had shown a significant effect

each one, and to draw inferences from several models simultaneously (Johnson and Omland 2004). Note that three unsexed individuals were excluded from the model selection process to ensure that all models were fitted to exactly the same set of data. This is a prerequisite for valid model comparison by information criteria (Burnham and Anderson 2002). We used a second order derivative of Akaike's Information Criterion (AIC_c), which contains a bias correction term for small sample size (number of free parameters exceeds $\sim n/40$; Burnham and Anderson 2002). Models were ranked according to the model with the lowest AIC_c , and the difference (ΔAIC_c) between the AIC_c value for the best model and the value for every other model was used to evaluate the relative plausibility of each model. Models within 2 AIC_c values of the best model were considered competitive and receive substantial support. For a model with ΔAIC_c 2–4, 4–7, and 7–10, there is definite evidence, weak evidence, and no evidence, respectively, that the model is the best approximating model (Burnham and Anderson 2002). We then calculated Akaike weights (ω_i) to determine the relative likelihood of each model given the data. The relative importance of individual parameters was examined by summing Akaike weights over all models containing the variable of interest. If there is no unambiguously best supported model ($\omega_i > 0.9$) in the set of candidate models, a model averaging approach over models containing the variables of interest is recommended (Burnham and Anderson 2002; Johnson and Omland 2004). Therefore, we adjusted Akaike weights only for models considered competitive and calculated model-averaged parameter estimates by multiplying explanatory variable coefficients with the model's Akaike weight and summing these products over competitive models. To assess reliability and precision, unconditional standard errors and confidence intervals were generated from the model-averaged parameter estimates following Burnham and Anderson 2002.

All statistical analyses were performed using SPSS 15.0 for Windows and the R environment version 2.7.0. (Crawley 2007; R Development Core Team, 2008).

Results

Of 239 post-fledglings (males: 46%, $n = 108$; females: 54%, $n = 128$; 3 unsexed) registered and weighed after fledging in 2000 and 2001, 106 returned as prospectors from 2002 through 2006 (see Table 1 for numbers and sex proportions). The return rates of these post-fledglings of the cohort 2000 (43.2%) and 2001 (44.9%) did not differ significantly ($\chi^2 = 0.065$, $P = 0.799$).

Is there any suggestion that post-fledging characteristics are associated with the fate of the subadults? In 2000,

males that returned to their natal colony site tended to leave the colony area when younger than returned females (Table 1). In contrast, in 2001, returned females instead showed the tendency to leave the colony at a younger age than males (Table 1). Hatch date did not differ between returned and non-returned individuals. Last post-fledging mass in prospectors of the 2001 cohort was approximately 5 g higher than in non-returned fledglings. In 2000, no difference was evident (Table 1).

We found a significant positive correlation between last post-fledging mass and departure age ($r = 0.275$, $n = 239$, $P < 0.01$). Further, we found a significant negative correlation between hatch date and departure age ($r = -0.304$, $n = 239$, $P < 0.01$). Last post-fledging mass and hatch date showed no correlation ($r = 0.072$, $n = 239$, $P = 0.269$).

Is the return probability of a fledgling predicted by its post-fledging characteristics? The best approximating model in the candidate set contained only the main effect of last post-fledging mass (Table 2). The top ranked candidate model had just 27% of the Akaike weights (Table 2), indicating that there was considerable uncertainty as to

Table 2 Model selection results for the return of subadult Common Terns natal to the Banter See colony, Wilhelmshaven, Germany, in two contrasting breeding seasons, 2000 and 2001

Model id	Model term	K	$\log(L)$	ΔAIC_c	ω_i	Deviance
1	LPFM	3	-159.47	0.00	0.27	318.93
2	YEAR + LPFM	4	-159.39	1.91	0.11	318.77
3	LPFM(YEAR)	4	-159.43	2.00	0.10	318.86
4	YEAR \times LPFM	5	-158.43	2.08	0.10	316.85
5	FM	3	-160.88	2.82	0.07	321.75
6	LPFM \times HD	5	-158.82	2.87	0.07	317.64
7	SEX \times LPFM	5	-158.87	2.96	0.06	317.73
8	SEX	3	-161.32	3.71	0.04	322.64
9	NULL	2	-162.36	3.74	0.04	324.72
10	LPFM \times DA	5	-159.30	3.83	0.04	318.61
11	HD	3	-161.92	4.90	0.02	323.83
12	SEX \times FM	5	-160.05	5.33	0.02	320.10
13	DA	3	-162.33	5.73	0.02	324.66
14	YEAR	3	-162.36	5.79	0.02	324.72
15	YEAR \times FM	5	-160.44	6.10	0.01	320.87
16	YEAR \times SEX	5	-161.12	7.47	0.01	322.24
17	YEAR \times DA	5	-161.43	8.09	0.00	322.86
18	YEAR \times HD	5	-161.65	8.52	0.00	331.29

Model terms include the main and first order interaction effects of year (YEAR), sex (SEX), departure age (DA), hatch date (HD), fledging mass (FM), and last post-fledging mass (LPFM), respectively. Models are ranked by ascending ΔAIC_c values with the best supported models at the top of the list

AIC_c for the best model was 325.04, K = number of estimable parameters including the intercept, the regression coefficient(s), and the variance, ω_i = Akaike weight

which of the highly ranked models was actually the best predictor of Common Tern survival. However, last post-fledging mass also appeared in other top ranked models, with a cumulative Akaike weight of 75% serving as an estimate of the relative importance of last post-fledging mass as predictor variable. Models 2–4 acquired mentionable support as they were roughly within two AIC_c values of the best supported model, indicating an interaction of last post-fledging mass with year (Table 2; Fig. 2). The coefficient estimates of model 4 were used to predict return probabilities presented separately for both years (Fig. 2): The return probability of post-fledglings of the 2001 cohort increased with their last post-fledging mass whereas in the cohort of 2000 this positive correlation was negligible.

The commonly used predictor variable fledging mass acquired only a cumulative 10% of Akaike weights and we found no evidence for an interaction with year (model 15, Table 2). All other models including the single main effects year, sex, hatch date, and departure age, respectively, received substantially less support. The relative importance weights of these parameters were confounded by their respective interaction term with last post-fledging mass accounting for the largest proportion of summed Akaike weights. Model-averaged parameter estimates and their unconditional standard errors (Table 3) were calculated using models 1–4 as they deviate only by two AIC_c units. The year effect was negative and its estimated 95% confidence interval (CI) widely bounded zero (Table 3) whereas the last post-fledging mass estimate was moderately imprecise and uncertain (CI: 0.050, -0.004 ; Table 3).

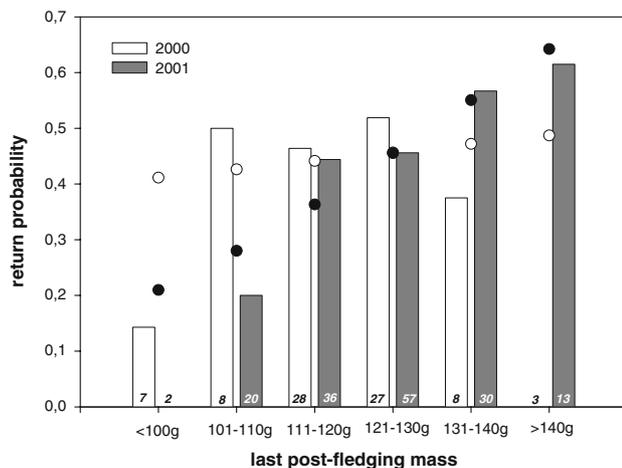


Fig. 2 Return probability of subadult Common Terns in relation to last post-fledging mass. Columns denote proportion of returned fledglings of the two cohorts (2000, 2001) in six body mass groups (n of each group at bottom of column). Dots (open circle = 2000, filled circle = 2001) represent the predicted probabilities for each group based on estimates from model LPFM × YEAR

Table 3 Model-averaged parameter estimates and their unconditional standard errors (SE) were calculated across models considered competitive (models 1–4)

Parameter	Estimate	SE	95% CI	
			Upper	Lower
Intercept	-2.988	1.687	0.318	-6.294
LPFM	0.023	0.014	0.050	-0.004
YEAR ₂₀₀₁	-1.984	2.652	3.213	-7.182

The weighted parameter estimates are based on regression coefficients on a logit scale

Intercept reflects the estimates for YEAR₂₀₀₀; given estimate for YEAR₂₀₀₁ states the difference between the 2000 intercept and the 2001 intercept

LPFM Last post-fledging mass, 95% CI 95% confidence interval

Discussion

Our results provide evidence of a significant influence of post-fledging body mass on the return rates of young Common Terns, but not with other post-fledging characteristics. We found strong inter-annual differences in all post-fledging characteristics indicating variation in environmental factors. Several studies have documented the crucial role of these factors in terms of breeding success and chick survival (e.g. Becker and Finck 1985; Becker and Specht 1991; Mlody and Becker 1991). While most of these studies focussed on detrimental environmental effects the chicks are exposed to during the nestling stage, it remained unclear whether these factors had consequences on further juvenile life stages. Recently, Schaubroth and Becker (2008) suggested that unfavourable conditions, as in 2000, also hamper post-fledging development and can cause higher mortality during the post-fledging stage. In 2000, many young were found dead after fledging, and those which survived did not significantly increase their body mass, which is essential in preparation for migration, until departure from the colony area (Schaubroth and Becker 2008). Under these circumstances, we considered these birds as handicapped and expected a year-effect due to higher mortality during migration. Similar return rates, however, did not indicate a year dependent effect on survival probability. Also, the survival rate of the 2000 cohort was only lower by 6.3% than in the subsequent cohort and was in the range reported for this colony (Becker et al. 2008).

In our study, last post-fledging mass was the only detected determinant of subsequent survival and thus an eligible predictor of return probability: the heavier the fledgling left the colony surroundings, the higher its survival probability. However, survival was not predicted by fledging mass. This trait or body condition before or at fledging, respectively, was used in most studies on

post-fledging survival, mainly due to methodological restrictions (Jarvis 1974; Hedgren 1981; Harris and Rothery 1985; Harris et al. 1992, 2007 for Common Guillemot *Uria aalge*; Sagar and Horning 1998 for Sooty Shearwater *Puffinus griseus*; Mougín et al. 2000 for Cory's Shearwater *Calonectris diomedea*; Feare 2002 for the Sooty Tern). The outcome of such studies greatly differed: while some reported a negative effect of low body mass at fledging on subsequent survival, others found no effect. Stienen and Brenninkmeijer (2002) predicted that the degree of post-fledging dependence on the parents might determine how fledging weight affects survival in seabirds, because all species for which a significant relationship between fledging weight and survival has been found become independent shortly before or directly after fledging. The Common Tern could be described as intermediate between shearwaters, which are independent at fledging (Sagar and Horning 1998; Mougín et al. 2000), and some auks, which leave the colony at a pre-fledging stage and benefit from prolonged parental care at sea during transition to independence (Hedgren 1981; Harris et al. 2007). Recently, Harris et al. (2007) reported strong inter-annual variation of first-year survival in Common Guillemots using data of 20 cohorts; however, they did not identify any covariates, including chick condition at fledging or environmental covariates, which could explain this variation. The authors suggest that juvenile survival is rather linked to parental quality as high-quality females tend to lay earlier in the season and high-quality males presumably are better able to prepare their chicks to survive their first winter at sea. At our study site, fledglings are fed by their parents at least for 6 weeks after fledging (Kühn and Becker, unpublished). During this period, Schaubroth and Becker (2008) did not find evidence for a relationship between fledging mass and post-fledging survival probability until departure from the colony.

Surprisingly, the last post-fledging mass of both returned and non-returned individuals of the 'poor' cohort 2000 showed no difference, whereas under favourable conditions in 2001 returned males as well as females were about 5 g heavier at post-fledging than those individuals that did not return (Table 1)—and these were even still heavier than the returned conspecifics of the cohort 2000. Obviously, the strength of the relationship between last post-fledging mass and survival probability is more pronounced in a 'good' year (Fig. 2). We speculate that this indicates selective mechanisms operating at different life stages regarding the two study years: In 2000, many individuals did not survive the pre-fledging as well as the post-fledging stage, therefore most 'weak' individuals were already eliminated prior to leaving the colony surroundings. Those individuals who survived the post-fledging period were the selected ones, but still of low body condition (see Fig. 2). On the other

hand, in 2001, environmental conditions were exceptionally favourable, causing high juvenile survival during both the pre- and post-fledging periods, as well as generally high body mass levels. Juveniles of lower quality therefore survived for the present, but may have died later in their life, during migration or wintering, when environmental constraints might have become critical.

In conclusion, this study underlines the importance of the post-fledging period for continuous mass gain in preparation for migration and its consequences for the future fate of young Common Terns. Our results suggest that last post-fledging mass could be used as predictor for survival and thus is a more relevant parameter than fledging mass, especially in species with prolonged parental care post-fledging.

Zusammenfassung

Die Körpermasse nach dem Ausfliegen als bestimmender Faktor für das Überleben subadulter Flussseseschwalben *Sterna hirundo*

In der der Forschung kaum zugänglichen Phase nach dem Ausfliegen gelangen uns Untersuchungen zum Einfluss von Merkmalen subadulter Flussseseschwalben auf ihr Überleben bis zur ersten Rückkehr zur Geburtskolonie im Alter von zwei Jahren. Dazu setzten wir ein durch Transponder automatisiertes Erfassungs- und Wägesystems an der Banter See Kolonie in Norddeutschland ein. Daten aus zwei gegensätzlichen Brutjahren, 2000 und 2001, lagen den Auswertungen zugrunde, um Jahres- und Geschlechtsunterschiede der Anwesenheitsdauer am Koloniestandort (Abflugalter), der Flügglingsmasse, der letzten registrierten Körpermasse vor dem Abflug sowie des Schlupftermins hinsichtlich möglicher Effekte auf die Überlebensrate zu prüfen. Unter Verwendung eines informationstheoretischen Ansatzes der Modellselektion zeigte sich, dass weder das Abflugalter noch der Schlupftermin die Überlebenswahrscheinlichkeit beeinflussten. Einzig die letzte registrierte Körpermasse hatte einen Einfluss auf das Überleben, während die Flügglingsmasse selbst von untergeordneter Bedeutung war. Obwohl sich eine schwache Interaktion zwischen der letzten registrierten Körpermasse und Jahr andeutete, wiesen Individuen des Jahrgangs 2000, die den Koloniestandort im Mittel 5 g leichter verließen als die unter günstigen Bedingungen aufgewachsenen Jungen des Jahres 2001, keine geringere Rückkehrwahrscheinlichkeit auf als letztere. Wir erklären diesen Befund mit Selektion: Schwache Individuen sterben bei ungünstigen Bedingungen bereits vor oder kurz nach dem Ausfliegen. Diese Studie unterstreicht die Bedeutung der Periode unmittelbar nach dem Ausfliegen, die besonders bei Arten mit

verlängerter elterlicher Betreuung Konsequenzen für die weitere Entwicklung und das Überleben der subadulten Tiere haben kann.

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