

Reproductive parameters in relation to food supply in the whiskered tern (*Chlidonias hybrida*)

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Received: 10 April 2006 / Revised: 13 September 2006 / Accepted: 10 October 2006 / Published online: 11 November 2006
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Abstract It is generally accepted that breeding terns are sensitive to food supply and that their reproductive effort could be substantially affected by the availability and access to resources. In this study we examined reproductive parameters in the whiskered tern *Chlidonias hybrida* in relation to food supply during the courtship feeding period (food brought by males to females) over a 2-year period (2004–2005). We also studied whether the condition of the nestlings [body condition index (BCI)] was related to a proxy of the reproductive investment of the adults (the clutch size) during a season of food shortage. Behavioural observations showed a decrease in the intensity of male courtship feeding between years (2004 > 2005), and a strong shift in the relative abundance of the two prey groups (invertebrates/fish; invertebrate prey dropped from 88.0 to 49.3%) brought by males. This change in food delivery rates did not result in a delay in laying, but there was a significant difference in mean clutch size between years (2.71 ± 0.49 eggs in 2004 and 2.05 ± 0.78 eggs in 2005) without any within-year variation in relation to the laying dates. The egg size (volume and length) was related to the year (2004 < 2005), suggesting a trade-off in the quantity

and the quality of eggs between the two seasons. We also found no evidence that the investment in a large clutch affected nestling BCI in the course of the food shortage season. Since many pairs (about 60%) interrupted breeding during the incubation stage, we assumed that parents that succeeded in rearing nestlings in these conditions were probably ‘high-quality’ individuals. Our results therefore showed that whiskered terns are sensitive to the varying food conditions they experienced throughout the courtship period. The diversity of prey types could be a key factor in the reproductive investment of this tern species.

Keywords Body condition · *Chlidonias hybrida* · Clutch size · Courtship feeding · Egg size · Laying date

Introduction

The energy costs associated with breeding events are among the highest experienced by adult birds throughout their lifetime. Life-history theory suggests that parents should balance their investment in the production of young against their own chance of survival and reproduction in the future at each stage in their reproductive cycle (e.g. Stearns 1992). Given the costs and benefits of breeding, parent birds – particularly in long-lived species (Burger and Gochfeld 1991) – are expected to be prudent and to adjust their reproductive effort each breeding season in response to the environmental conditions they experience (Drent and Daan 1980; Monaghan et al. 1989; Svensson 1995). Many aspects of breeding events could be affected, such as attempting, or not, to breed, the timing of laying, clutch size and egg size, food provisioning to the nestlings and the

Communicated by P.H. Becker.

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probability of desertion (e.g. Monaghan et al. 1989, 1992; Robertson 1995; Cam et al. 1998; Christians 2002). Terns are of particular interest since the costs of egg production, which mainly come from their current dietary intake rather than from stored reserves, are particularly high in this bird family (Moore et al. 2000). Furthermore, despite some equivocal results (Safina et al. 1988; Monaghan et al. 1992), it is now generally accepted that courtship feeding performance of the male contributes significantly to the nutritional intake of the female and to the egg mass (Nisbet 1973; Wendeln 1997; Wendeln et al. 2000).

In the study reported here, we examined reproductive parameters in the whiskered tern *Chlidonias hybrida* over a 2-year study period. We analyzed if and in which way females adjusted their reproductive effort in response to the food brought by males throughout the courtship period. We also presented data on the food abundance in the feeding areas to provide a picture of the varying environmental conditions that the birds experienced throughout the breeding period. We predicted a positive relationship between the intensity of courtship feeding by males, in conjunction with food abundance and the reproductive parameters of females (egg size and clutch size) and changes in laying dates. Taking advantage of a period of food shortage, we also tested the effect of clutch size on the nestling body condition index (BCI). If parental care varies between breeding pairs, then either a positive relationship between clutch size and nestling BCI should be detectable or no significant relationship should be obtained. Conversely, if parental care is not an important parameter, then large clutches would induce additional costs. In this latter case, we would expect a negative relationship between clutch size and nestling BCI.

Methods

Study species, study site and environmental conditions experienced by whiskered terns

The whiskered tern is a cosmopolitan marsh species that is distributed throughout southern and central Europe, but its breeding distribution is scattered, and the species is usually restricted to small colonies established on floating vegetation (Tomialojc 1994; Gochfeld and Burger 1996; van der Winden 1997). Despite its unfavourable conservation status in Europe (Tomialojc 1994), the whiskered tern has been little studied (Spina 1982), although recently it has been the focus of two studies (Bakaria et al. 2002; Paillisson et al. 2006).

The present study was carried out during two breeding seasons (2004–2005) at Lake Grand-Lieu (47°05'N, 1°39'W), in western France. It is a very large shallow natural lake (4000 ha in the summer and up to 6300 ha in the winter) covered with extensive beds of floating plants (770–978 ha depending on the year) comprising mainly waterlily *Nymphaea alba* beds (58–67% of the floating vegetation area). Lake Grand-Lieu currently supports a whiskered tern breeding population ranging from 620 to 1250 pairs breeding at 10–11 colonies. Nesting platforms are always built on waterlily beds and consist mainly of waterlily leaves and stems and common clubrush *Scirpus lacustris* stems (Paillisson et al. 2006).

The whiskered tern is known to be an opportunistic feeder that eats a wide variety of prey, essentially invertebrates, small fish and possibly frogs (Dostine and Morton 1989; Gochfeld and Burger 1996). We investigated the food conditions during the courtship period in the 2 years of the study. Fish stocks in the spring feeding grounds of the terns were estimated by electrofishing using the point abundance sampling (PAS) method [see Carpentier et al. (2002) for details of the method]. We only took into account fish with a body length of less than 100 mm, which represent the maximum size of fish eaten by adult whiskered terns (Dostine and Morton 1989, and personal observations). Fish stocks were expressed in number of fish (<100 mm) per PAS. Field observations indicated that the most commonly eaten invertebrate prey (adult dragonflies and beetles, notably the chrysomelid *Gal-erucella nymphaeae*) were much less abundant during the courtship period in 2005 than in 2004. Even though we have only partial data on the food abundances, we assumed that the types of prey delivered to females and the provisioning rates are a good reflection of the food availability (this assumption has also been used in other studies; see Frank 1992).

Male activity during the courtship feeding period

Prey delivery rates by the males during the courtship period were registered by observations with a telescope from a distance of 50–100 m. In 2004 we examined 37 nests (30-min scan each nest; 7 days; May 25 to June 16) for a total observation time of 1110 min; in 2005, this was 83 nests (7 days; May 5 to June 9) for a total observation time of 2490 min. In both years we chose the nests at random in several colonies in order to have a representative sampling of male activity, and observations were undertaken throughout the daytime period (8–12 a.m. and 3–8 p.m.). We used a methodology derived from that of Altmann (1974) to register a bird's

activity (authors, unpublished data). Sexes were visually differentiated by bill size, as the bill of the males is larger than that of the females (Cramp 1985; Latraube 2006). At this breeding phase, females spend a large amount of their time on the nest [74% in 2004 ($n = 37$ nests) and 85% in 2005 ($n = 83$)], and males actively search for nest-building material and a food supply (absence time: 67% in 2004 and 56% in 2005; see details on the sample size presented above). The number of male arrivals on the nest (with or without food or plant materials) and food delivery to females were recorded. Data were calculated on an hourly basis. The very good observation conditions combined with the fact that terns generally bring back a single prey item in their bill allowed us to accurately determine the type of prey delivered to females on the nest: 95.6% of prey total in 2004 ($n = 122$) and 85.6% in 2005 ($n = 90$). Prey was classified into two groups: invertebrates and fish. Fish was identified to the species level if possible, but at least into three categories: cyprinids (breams *Abramis brama* and *Blicca bjoerkna*; rudd *Scardinius erythrophthalmus*; sunbleak *Leucaspis delineatus*), pike *Esox lucius* and pumpkinseed *Lepomis gibbosus*. Fish size was estimated with reference to the adult bill length. Since the energetic content of prey plays an important role in the reproductive performance of birds, fish prey delivered to females were also expressed as biomass (grams fresh weight, g FW) using in situ length/fresh mass relations defined for each fish group (Adam and Elie 1993). For the cyprinid group, the length/mass equation of rudd was used, based on the dominant position of this fish species in the study site.

Clutch size and egg size

To investigate reproductive parameters, we visited six to seven colonies weekly in 2004 and only once in 2005 (but at different dates from May 25 to June 16) during the incubation period to minimize disturbance. Whiskered terns are known to lay two- and three-egg clutches, the latter being more common (Cramp 1985; Bakaria et al. 2002). Egg size (length and width) was measured with a Vernier calliper to the nearest 0.1 mm, and egg volume (cm^3) was calculated using Coulson's (1963) equation: $\text{volume} = 0.4866 \times \text{length} \times \text{width}^2$. For the analyses, we used mean egg size of the clutch. Egg weight was measured using an electronic balance to the nearest 0.1 g. As in other bird species, the weight of the whiskered tern egg decreases with egg age. We therefore used an in situ linear egg density/age relationship determined in 2004 [$\text{age (day)} = -107.33 \times \text{density (g/cm}^3) + 117.95$;

$r^2 = 0.77$; $n = 188$ measurements of eggs of known laying or hatching dates considering an average incubation duration of 20 days (Cramp 1985; Gochfeld and Burger 1996; Bakaria et al. 2002)]. Based on this relationship we determined the clutch initiation date (i.e. the laying date of the first egg) and recorded whether one- and two-egg clutches measured in 2005 were complete, knowing that an interval of at least 1 day is necessary between the laying of successive eggs. Some clutches measured in 2005 (2.95%, $n = 406$) that could not be accurately defined as complete from the estimation of the egg age using egg measurements performed at the first visit in each colony were visited a second time (1 week later) to verify the clutch size and to measure any additional eggs. For the analyses, laying dates were expressed in pentades (i.e. time intervals of 5 days, beginning with May 1). Residual laying dates [calculated by subtracting individual's laying date (in pentades) from the peak laying date of all nests: pentade 8 in 2004 and pentade 7 in 2005) were used to eliminate year effects and compare seasonal patterns of laying date. For the comparison of clutch size and egg size as the season progresses, residual laying dates were classified into three classes: peak laying (within the three pentades of peak laying), early laying (before peak laying; -2 in 2004 and -2, -3, -4 in 2005) and late laying (after peak laying, 2, 3, 4 in 2004 and 2, 3 in 2005).

Nestling body condition index

Nestlings from 61 nests ($n = 86$) were measured in mid-July in 2005 in one colony at night to limit the disturbance to the nests and to minimize the bias arising from large variations in the body weight of nestlings that occurs during the daylight period when chicks are fed. Catching operations were performed using a non-motorized boat and an handheld spotlight which enabled us locate nestlings on nests at a distance that can largely exceed 100 m. When a brood was located, the spot light was always directed towards it until the operators reached the nest, thereby preventing the risk of error in the determination of the brood size and the allocation of chicks to a specific nest. Indeed, even if the nestlings generally stayed on the nesting platform, some individuals sometimes tried to run away or hide under waterlily leaves when we approached. Since the aim of the study was to investigate nestling BCI in relation to clutch size, two broods were removed from the data set after the discovery of one dead nestling on the nest. Nestlings were measured at an age ranging from 6 to 17 days (estimation derived from a logistic wing length/age regression; authors unpublished data). According to the recommendations

of Jakob et al. (1996) and Green (2001), the first step in calculating a BCI consists in performing a principal component analysis (PCA) on several body size variables (here we used wing, tarsus and culmen lengths ± 1 mm). The second step consists in using residuals (relative deviation) drawn from a regression between the structural measure of body size (log-transformation of each variable) and body weight (± 0.1 g, log-transformed) as a BCI. Component scores on the first axis of the PCA (PC1) explained 80.1% of the variation in nestling body size, and nestling body weight was positively related to PC1 scores [linear regression: $\log(\text{body weight}) = 0.033 \text{ PC1} + 1.86$; $r^2 = 0.56$, $F_{1,83} = 100.68$, $P < 0.001$]. The assumption of linearity of residuals (Green 2001) was visually inspected, and the addition of a quadratic term to the regression did not substantially improve r^2 (0.60). For the investigation of the effect of clutch size on nestling BCI, we used the mean BCI of the brood if this had more than one nestling in order to avoid dependent data for the statistical analysis.

Data analysis

Values are means \pm standard deviation (SD). Assumptions of normality and homoscedasticity were tested using the Kolmogorov-Smirnov/Lilliefors test and Bartlett's test. When deviations from normality were detected, non-parametric ANOVA (Mann-Whitney) tests were performed. The PCA on nestling body size was performed using ADE-4 software (Thioulouse et al. 1997), and statistical analyses were conducted using STATISTIX (version 8.0) and SYSTAT (ver. 9.0; SPSS 1999). Tests were two-tailed, and $P \leq 0.05$ was taken as level of significance.

Results

Food availability and intensity of courtship feeding

Although the activity of males (arrival rates on the nest) was lower in 2004 than in 2005, the food delivery rate was twofold higher (Table 1). The food delivery rate represented 67.9% of all male arrivals on the nest in 2004 and only 23.3% in 2005. The type of prey delivered to females on the nest also varied greatly between years, with invertebrate prey comprising a larger proportion of total prey delivered to females in 2004 (88.0%, $n = 117$ identified prey) than in 2005 (49.3%, $n = 77$ identified prey; Fisher's exact test = 34.99, $P < 0.001$). In contrast, fish delivery rates (number and biomass) and fish stocks

in spring feeding areas were similar in both years (Table 1).

Reproductive parameters and nestling body condition index

Whiskered terns laid significantly earlier in 2005 (May 4 ± 6 days) than in 2004 (May 10 ± 7 days; two-sample t test, pooled variance $t = 7.57$, $df = 597$, $P < 0.001$) but not more synchronously (two-sample Kolmogorov-Smirnov, $KS = 0.33$, $P = 0.66$; Fig. 1). In 2004, three-egg clutches represented 73.0% of all clutches and one-egg clutches only 1.9% (Table 2). Conversely, three-egg clutches only represented a third of all clutches in 2005 (33.5%), whereas one-egg clutches increased to 27.8% (Table 2). Consequently, the average clutch size significantly decreased from 2.71 ± 0.49 eggs in 2004 to 2.05 ± 0.78 eggs in 2005 (two-sample t test, pooled variance $t = 10.92$, $df = 615$, $P < 0.001$). Clutch size did not vary throughout the laying period in either year (Table 3).

The egg size (volume and length) was related to the year but not to the clutch size (all interactions were non-significant, as assessed by GLM; Table 4). Both the egg volume and egg length were significantly higher in 2005 than in 2004 (see values in Table 2). The egg width did not differ with any of the independent variables (Table 4). Egg size did not vary throughout the laying period in 2004, whereas some differences were found in 2005 (Table 3): egg width and egg volume were significantly larger during the peak laying period than in the late laying period (pair-wise comparisons, Tukey HSD procedure, $P = 0.01$ and $P = 0.02$, respectively). No difference was found for egg length in relation to laying dates in 2005 (Table 3).

The nestling BCI determined in the year of poor food supply (2005) was similar between clutch sizes (non-parametric ANOVA, Kruskal-Wallis, $KW = 1.16$, $P = 0.56$, $n = 59$ broods; Fig. 2).

Discussion

During the course of this study we found that females were much less well provisioned by males in 2005 than in 2004; more specifically, they were supplied with fewer invertebrates. This occurred in the period with the lowest minimum daily air temperature reported for the study area during the last 10 years (1995–2005), which was 4.2° and 4.6°C lower than the mean temperature calculated for April and May, respectively (data from the Bouguenais meteorological station located 5 km from the breeding site). Given that

Table 1 Comparison of the activity of the males (number of arrivals at the nest, food delivery^a, number and biomass of fish delivered^b, all on a per hour basis) and fish abundance at the feeding grounds^c during the courtship period in 2004 and 2005

Variable	Mean ± SD		One-way ANOVA		
	2004	2005	<i>n</i> ^d	<i>U</i> or <i>F</i>	<i>P</i>
Number of arrivals/h	7.07 ± 2.32	10.68 ± 1.46	120	1110	0.01
Food delivery rate/h	5.03 ± 2.25	2.49 ± 0.74	120	1095	0.004
Number of fish delivered/h	0.76 ± 0.18	0.94 ± 0.25	120	1614	0.58
Biomass of fish delivered (g FW)/h	1.61 ± 0.53	1.98 ± 0.38	120	1376	0.32
Number of fish/PAS	1.74 ± 0.22	2.18 ± 0.17	197	2.58	0.11

^a Food delivery: Number of all prey items brought to the female at the nest

^b Biomass is expressed in grams fresh weight

^c Number of fish per point abundance sampling (PAS)

^d *n* = Number of scans (37 in 2004, 83 in 2005) and number of PAS (80 in 2004, 117 in 2005). See the text for details on the methodology

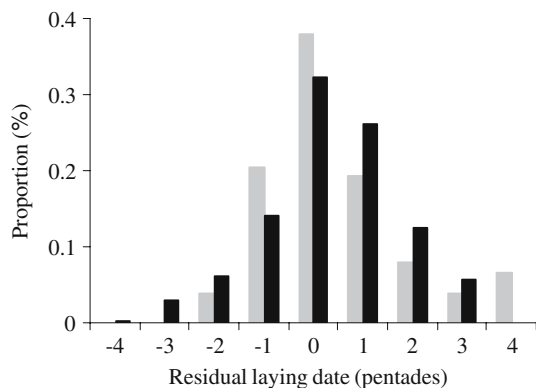


Fig. 1 Temporal pattern of clutch initiation (first egg laid), expressed as a percentage of the total number of clutches, in relation to laying dates. Grey square 2004 (*n* = 211), black square 2005 (*n* = 406). See the text for details on the calculation of laying dates

temperatures affect the timing of emergence of aquatic invertebrates (Williams and Feltmate 1992), we assume that these low temperatures reduced the availability of aquatic invertebrates in 2005, thereby limiting the amount of invertebrates supplied by whiskered tern

males to their females during this period. However, invertebrates were not replaced by fish in the diet (no significant increase in the number and biomass of fish delivered; Table 1). The reason for the low compensation by fish in the diet of females remains unexplained. It might result from the selection of a less energy-costly foraging method by males in these adverse conditions: the picking up, surface feeding or pursuing of invertebrate prey are activities which individually probably cost less energy than plunging to catch fish. Another explanation may be that fish avoided the upper part of the water column as it was too cold. Under these conditions, the similar fish delivery rates observed between the 2 years might be related to a higher energetic investment of males in 2005. Despite the lower energetic values of invertebrate prey compared to fish [see, for example, the review of intake values in Van der Winden (2005)], the consumption of invertebrates seems to be an important factor in the reproductive performance of the breeding whiskered terns at the egg development period. This may be related to the fact that invertebrates can be caught efficiently in the vicinity of the nesting areas (waterlily

Table 2 Egg size (mean ± SD) in relation to clutch size in the 2-year study period

Egg size	Clutch size (number of eggs)			
	1	2	3	Total
2004				
Length (mm)	38.59 ± 2.10	38.19 ± 1.50	38.71 ± 1.32	38.57 ± 1.39
Width (mm)	28.12 ± 0.57	27.91 ± 0.80	27.98 ± 0.69	27.97 ± 0.72
Volume (cm ³)	14.85 ± 0.85	14.50 ± 1.14	14.77 ± 1.02	14.70 ± 1.05
<i>n</i> ^a	4	53	154	211
2005				
Length (mm)	39.23 ± 1.66	39.04 ± 1.61	39.19 ± 1.40	39.14 ± 1.55
Width (mm)	28.19 ± 0.77	28.12 ± 0.69	28.08 ± 0.71	28.13 ± 0.72
Volume (cm ³)	15.19 ± 1.21	15.04 ± 1.07	15.06 ± 1.05	15.09 ± 1.10
<i>n</i> ^a	113	157	136	406

^a *n*, Number of clutches

Table 3 Comparison of clutch size and egg size (mean \pm SD) in relation to laying dates in the two seasons^a

Variable	Mean \pm SD			One-way ANOVA		
	Early	Peak	Late	<i>n</i> ^b	<i>F</i>	<i>P</i>
2004						
Clutch size	3.00 \pm 0.00	2.69 \pm 0.51	2.74 \pm 0.44	211	1.62	0.20
Egg length (mm)	38.99 \pm 1.13	38.59 \pm 1.48	38.44 \pm 1.05	211	0.54	0.58
Egg width (mm)	27.87 \pm 0.54	27.95 \pm 0.77	28.06 \pm 0.51	211	0.42	0.66
Egg volume (cm ³)	14.75 \pm 0.77	14.69 \pm 1.12	14.74 \pm 0.79	211	0.04	0.96
2005						
Clutch size	2.00 \pm 0.80	2.00 \pm 0.79	2.22 \pm 0.76	406	2.24	0.11
Egg length (mm)	38.94 \pm 1.47	39.22 \pm 1.57	38.96 \pm 1.52	406	1.27	0.31
Egg width (mm)	28.14 \pm 0.72	28.18 \pm 0.72	27.90 \pm 0.69	406	4.27	0.01
Egg volume (cm ³)	15.03 \pm 1.03	15.17 \pm 1.13	14.78 \pm 0.97	406	3.90	0.02

^a Residual laying dates converted in the three classes. See the text for details on the methods

^b *n*, Number of clutches

Table 4 Effects^a of year and clutch size on egg size

	Independent variables		
	Year	Clutch size	Year \times clutch size
Egg length	5.81**	2.56 NS	0.75 NS
Egg width	0.88 NS	0.30 NS	0.35 NS
Egg volume	3.89*	1.07 NS	0.72 NS

P* = 0.05, *P* = 0.01; NS, not significant

^a The results of the GLM procedures are presented: *F* values (*df* = 1 for year and *df* = 2 for clutch size and for year \times clutch size in all analyses; *n* = 617 clutches)

beds). More generally, the diversity of prey types could be a key factor in the reproductive investment of this tern species throughout the courtship period.

When adult terns face poor feeding conditions early in the breeding season, they generally delay laying [Nisbet (1977) in common terns *Sterna hirundo*; Safina

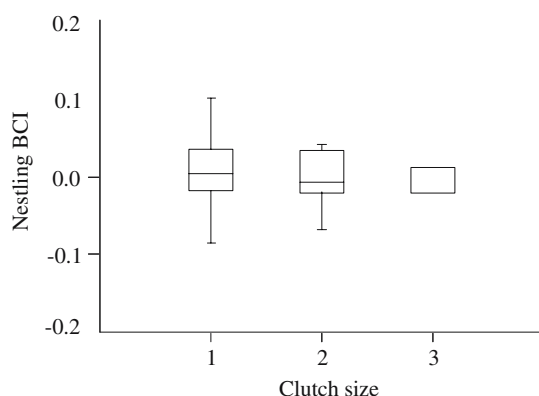


Fig. 2 Nestling body condition index (BCI) in relation to clutch size in 2005. Mean values are shown as horizontal lines, the length of the box represents SD and the length of the bars are the range of values. See the text for details on the calculation of BCI

et al. (1988) in common and roseate *S. dougallii* terns; but no effect was found by Monaghan et al. (1992) in arctic terns *S. paradisaea*]. In the present study, whiskered terns did not delay laying in response to prey limitation. In contrast, they laid slightly earlier in 2005 than in 2004. Moreover, the timing of laying in whiskered terns has been found to be strongly affected by other proximate factors, such as the development of floating plant beds and the water level conditions (Paillisson et al. 2006). However, we found no sign that the development of waterlily beds in 2005 had a positive effect in enabling the birds to breed early in 2005 despite the food shortage. In May, the waterlily biomass was 128 ± 36 g DW m⁻² in 2004 and 121 ± 25 g DW m⁻² in 2005 (J.-M. Paillisson, unpublished data). However, the number of breeding pairs had greatly increased in 2005 (1248 pairs and 694 pairs in 2004), and possible competition for nest sites could explain the early onset of breeding in 2005 despite the less suitable breeding conditions. Because in both study years no variation occurred in the clutch size as the season progressed, laying later would not be an advantageous strategy since birds most likely have no knowledge of future feeding conditions. In general, egg size decreases during the course of a breeding season because late clutches are mainly replacement clutches or clutches produced by young, inexperienced or low-quality birds (Coulson and Thomas 1985; Wendeln 1997), or they may coincide with a decline in food availability (Parsons 1975; Sydeman et al. 1991). This was probably the case in the present study in 2005, since egg size was smaller in late clutches. On the other hand, the absence of a relationship between egg size and laying dates in 2004 suggests that food resources were available in sufficient quantity throughout the season and did not affect late whiskered tern breeders.

When food supply is insufficient, it may be less adaptive to invest the available resources in an extra egg (Drent and Daan 1980; Becker et al. 1985); conversely, it may be a better strategy to invest in relatively fewer and larger eggs which have generally been shown to have a higher probability of survival (see, for example, Quinn and Morris 1986; Bolton 1991; Hipfner 2000). This trade-off between the quantity and the quality (size) of eggs was found in the present study: large clutch size was linked with relatively small eggs in 2004, and small clutch size was linked with large eggs in 2005.

In the present study, we also explored whether the body condition of the nestling was related to clutch size in the period of food shortage. We found that nestlings from large broods had a similar BCI as those from one-chick broods despite increased costs for the parents. The capacity to produce an extra egg and to rear an additional chick without any negative influence on the chick development (particularly when food conditions are poor) is considered to be dependent on the parents' quality. Indeed, clutch size is among the parameters that generally reflect high levels of parental quality (Coulson and Porter 1985). Consequently, breeding pairs that succeeded in rearing large broods in 2005 could be defined as high-quality parents. Possible increases in food quantity and quality as the season progressed (that is, after the laying period) could also account for the good performance in large broods. In other respects, breeding success is the final surrogate for parental effort. Although this reproductive parameter was not investigated in the present study, we found that many pairs (about 60%, $n = 70$) interrupted breeding during the incubation stage in 2005, whereas the hatching success (the number of nests with chicks (<5 days) as a percentage of the total number of nests) was 70% in 2004. Massive interruption of incubation is known in this species when poor weather conditions occur, such as flooding episodes (Tomialojc 1994). However, this was not the case in the study period, and no other factors are known to induce such a high desertion rate during incubation in the study site. Therefore, we suggest that this high level of breeding failure is consistent with the hypothesis that the parent birds, faced with poor food conditions after clutch completion, deserted the nests early during the breeding period to avoid an increased risk of mortality (e.g. Monaghan et al. 1992; Chaurand and Weimerskirch 1994). In this context, our results suggest that parents that succeeded in rearing chicks in 2005, whatever the brood size, were birds of high 'condition' or 'quality'. Our current approach does not allow us to investigate other parameters of whiskered terns'

reproductive performance – either as a group or on the level of the individual, and its changes over time and fluctuating environmental conditions.

Zusammenfassung

Reproduktive Parameter der Weißbartseeschwalbe (*Chlidonias hybrida*) in Beziehung zum Nahrungsangebot

Brütende Seeschwalben reagieren sensitiv auf das Nahrungsangebot, und der reproduktive Aufwand kann durch die Nahrungsverfügbarkeit und den Zugang zu Nahrungsquellen erheblich beeinflusst werden. In dieser Studie untersuchten wir reproduktive Parameter der

Weißbartseeschwalbe *Chlidonias hybrida* in Beziehung zum Nahrungsangebot während der Balzfütterungsphase (die Männchen versorgen ihre Weibchen mit Nahrung) zweier Jahre, 2004–2005. Außerdem prüften wir, ob während einer Saison mit Nahrungsmangel die Kondition der Nestlinge (Konditionsindex BCI) in Zusammenhang stand mit der Gelegegröße als Maß für die reproduktive Investition der Eltern. Verhaltensbeobachtungen zeigten eine Abnahme der Intensität der Balzfütterungen mit den Jahren (2004 > 2005) und eine starke Verschiebung in der relativen Häufigkeit der von den Männchen übergebenen Nahrungstiergruppen Invertebraten und Fische (der Anteil an Invertebraten fiel von 88,0 auf 49,3%). Der Unterschied in den Fütterungsraten hatte keine Verzögerung der Eiablage, jedoch einen signifikanten Unterschied der Gelegegröße beider Jahre zur Folge ($2,71 \pm 0,49$ Eier in 2004, $2,05 \pm 0,78$ Eier in 2005), ohne dass innerhalb der Jahre saisonale Unterschiede festgestellt wurden. Die Eigröße zeigte in Volumen und Länge gegenläufige Jahresunterschiede (2004 < 2005), was einen Kompromiss zwischen Anzahl und Qualität der gelegten Eier andeutet. Wir fanden auch keinen Hinweis, dass die Investition in ein großes Gelege die Nestlingskondition (BCI) während der durch Nahrungsknappheit gekennzeichneten Saison beeinflusste. Da viele Paare (ca. 60%) die Bebrütung ihres Geleges abgebrochen hatten, nehmen wir an, dass Eltern mit Nestlingen, die unter diesen Bedingungen erfolgreich aufgezogen wurden, sicherlich Altvögel von „hoher Qualität“ waren. Unsere Ergebnisse zeigen, dass Weißbartseeschwalben während der Balzfütterungsperiode sensitiv auf die variablen Nahrungsbedingungen reagieren. Die Diversität der Nahrung könnte eine Schlüsselfunktion für den Reproduktionsaufwand dieser Seeschwalbenart einnehmen.

Acknowledgements The research was carried out under licence of the Prefecture de la Loire-Atlantique (DAIE, Bureau de la Réglementation de l'Environnement) and of the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux). We are grateful to Réserve Naturelle du Lac de Grand-Lieu for giving us access to this site. M. Guillemain (ONCFS) and F. Latraube (CEBC) kindly allowed us access to the *Focal Sampler* macro for analysing bird behaviours. Part of the study was funded by SNPN and the Université de Rennes. The comments of C. Barbraud, P.H. Becker, V. Bretagnolle, M.-C. Eybert, F. Latraube, J. van der Winden and an anonymous reviewer considerably improved the manuscript. We also thank R. Britton for linguistic improvements.

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