

Sex-specific vulnerability to breeding conditions in chicks of the sexually monomorphic Gull-billed Tern

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Abstract Environmental conditions during early development may differentially affect male and female offspring, and the effects of this sex–environment interaction in chick performance may be exaggerated under harsh conditions. In birds, most of the currently available evidence on sex-biased environmental sensitivity in nestlings is derived from species that display sexual size dimorphism, while studies on monomorphic or slightly dimorphic species are less abundant and have produced inconsistent results. We have evaluated sex-specific vulnerability to breeding conditions in chicks of the Gull-billed Tern (*Gelochelidon nilotica*), a semiprecocial species with only low sexual size dimorphism. We compared male and female mass growth and fledgling physiological condition (measured through plasma metabolite levels) in several colonies that differed in reproductive parameters. Chicks of both sexes grew more slowly and fledged with lower mass and poorer nutritional state in the colony with the worst breeding conditions, i.e., with later phenology and lower clutch size and reproductive success. Contrary to our expectations, chick vulnerability to rearing conditions was more pronounced for female than male fledglings. While males grew faster than females during the middle phase of growth regardless of colony, this difference disappeared later in the fledging period in all but the worst colony, where females maintained a lower mass and worse nutritional condition than males. These results add to the

evidence that, even in monomorphic species, the environmental sensitivity of nestlings during development may vary in a sex-specific way that may select for sex-biased allocation of parental resources and sex ratio adjustments under specific breeding conditions.

Keywords Chick growth · Environmental sensitivity · Physiological condition · Plasma metabolites · Sex–environment interaction · Sexual dimorphism

Zusammenfassung

Geschlechtsspezifische Anfälligkeit gegen Aufzuchtbedingungen bei Küken eines sexuell monomorphen Vogels, der Lachseeschwalbe

Die Umweltbedingungen während der frühen Entwicklung können männliche und weibliche Nachkommen unterschiedlich beeinflussen, und diese Geschlechts-Umwelt-Interaktion in der Kükenperformanz kann unter harschen Bedingungen verstärkt sein. Bei Vögeln stammen die meisten Belege für geschlechtsspezifische Umweltempfindlichkeit aus Arten mit sexuellem Größendimorphismus, während Untersuchungen an monomorphen oder nur leicht dimorphen Arten seltener sind und widersprüchliche Ergebnisse erbracht haben. Hier schätzen wir die geschlechtsspezifische Anfälligkeit gegen die Aufzuchtbedingungen bei Küken der Lachseeschwalbe (*Gelochelidon nilotica*) ab, einer halb-nestflüchtenden Art mit nur geringem sexuellen Größendimorphismus. Wir haben den Körpermassezuwachs von Männchen und Weibchen und ihre physiologische Kondition als Flügglinge (gemessen über den Plasmametabolitspiegel) in mehreren Kolonien, die sich in Fortpflanzungsparametern unterschieden, verglichen. Küken beider Geschlechter wuchsen langsamer und wiesen beim Ausfliegen eine geringere

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Körpermasse und einen schlechteren Ernährungszustand auf in der Kolonie mit den schlechtesten Brutbedingungen, d.h. mit späterer Phänologie, kleinerer Gelegegröße und niedrigerem Fortpflanzungserfolg. Entgegen unserer Erwartungen waren weibliche Küken empfindlicher gegen die Aufzuchtbedingungen als männliche. Während Männchen in der mittleren Wachstumsphase schneller wuchsen als Weibchen, unabhängig von der Kolonie, verschwand dieser Unterschied später in der Ausflugsperiode in allen Kolonien außer der schlechtesten, wo Weibchen weiterhin eine geringere Körpermasse und einen schlechteren Ernährungszustand als Männchen aufwiesen. Diese Ergebnisse liefern weitere Belege, dass selbst bei monomorphen Arten die Umweltempfindlichkeit der Nestlinge während der Entwicklung geschlechtsspezifisch variieren kann, was unter bestimmten Brutbedingungen eine verstärkte Zuteilung elterlicher Ressourcen zu einem Geschlecht sowie eine Anpassung des Geschlechterverhältnisses der Nachkommen begünstigen kann.

Introduction

Parents are expected to maximise fitness by distributing limited resources among progeny members according to their expected reproductive value (Stearns 1992). Sex is assumed to be an important source of variation in nestling relative fitness benefits because males and females may have differential access to reproduction or differ in susceptibility to environmental conditions (Hardy 2002). Such sex differences in the relative fitness prospects of rearing either sons or daughters are expected to influence the allocation of parental care and may select for sex ratio adjustments in relation to maternal or environmental conditions at the time of breeding (Trivers and Willard 1973).

Sons and daughters may have different requirements or optima with respect to resources or environmental conditions, and this sex–environment interaction in offspring performance may be exaggerated when these conditions deteriorate (Kalmbach and Benito 2007; Jones et al. 2009). Several hypotheses have been proposed to explain this differential environmental susceptibility of the sexes (Jones et al. 2009). Male and female offspring may have different food demands because of strong sexual size dimorphism, but this may also be the case in size monomorphic species as a consequence of early-established differences in offspring physiology that could result in differential food assimilation rate or daily energy expenditure (Vedder et al. 2005). Other size-independent traits, such as higher levels of testosterone in males, which may negatively impact on immunocompetence (Owen-Ashley et al. 2004), or the lower resistance to parasite infections of the heterogametic

sex (Washburn et al. 1965), have also been proposed as being responsible for differences in vulnerability between sexes. Furthermore, sex may also be a powerful determinant of competitive asymmetry among siblings, as offspring of different sex may differ in traits relevant for individual success in sib–sib competition (Uller 2006).

In birds, most of the evidence that is currently available on sex-biased environmental sensitivity in terms of nestling growth and survival is derived from species that have sexual size dimorphism, where the general pattern is that the larger sex suffers more pronounced negative consequences when rearing conditions deteriorate, owing to their greater nutritional requirements (e.g. Nager et al. 2000; Velando 2002; Laaksonen et al. 2004; Kalmbach et al. 2005). However, studies on the sex-specific effects of rearing conditions in species with a small degree of sexual size dimorphism are less abundant and are characterised by inconsistent results. While some of these studies did not find sex-specific vulnerability to adverse conditions during growth (e.g. Sheldon et al. 1998; Harding et al. 2009), in others either females (Råberg et al. 2005; Rowland et al. 2007) or males (Fletcher and Hamer 2004; Rosivall et al. 2010) were more sensitive to unfavourable rearing conditions. Accordingly, more data on sex-specific vulnerability to environmental conditions in nestlings of monomorphic or slightly size dimorphic species could add new insights into the relative fitness benefits of rearing sons and daughters and how these influence parental decisions on sex allocation and brood sex ratio adjustment under contrasting breeding conditions.

The Gull-billed Tern (*Gelochelidon nilotica*) is a semi-precocial migratory bird with negligible sexual size dimorphism: adult males are approximately 4 % larger than females in terms of bill, tarsus and body mass (Sánchez-Guzmán and Fasola 2002). Villegas et al. (2005) found variations in fledgling sex ratio according to colony breeding characteristics in this species, with a greater proportion of male fledglings found in colonies with greater mean clutch size. These results suggest that in this species male and female chicks could have a different fitness return and/or survival prospects according to environmental conditions, causing either a higher production of males under favourable breeding conditions or a higher mortality of males when these conditions deteriorate (Hardy 2002).

In our study, we evaluated sex-specific susceptibility to environmental conditions in Gull-billed Tern chicks, comparing patterns of male and female chick performance in several colonies that differed in reproductive parameters. As indicators of chick performance we considered mass growth rate and physiological condition of the fledgling, evaluated through the analysis of three plasma metabolites: uric acid, triglycerides and plasma alkaline phosphatase

(ALP). These plasma metabolites have been previously related to nutritional state and growth performance in nestlings of this and other bird species (e.g. Villegas et al. 2002; Tilgar et al. 2004; Albano et al. 2011a). Based on previous findings in this and other tern species (Becker and Wink 2003; Fletcher and Hamer 2004; González-Solís et al. 2005; Villegas et al. 2005), we hypothesise that males are more expensive to rear and more vulnerable to adverse conditions during growth than females. Thus, they should benefit more from growing up under favourable environmental conditions, while females should do better than males under detrimental conditions.

Materials and methods

Study area and data collection

This study was performed in Extremadura, southwestern Spain, where the Gull-billed Tern breeds regularly (about 1,100 pairs; Corbacho et al. 2009) on islands situated in large reservoirs (Sánchez-Guzmán et al. 2004). Six independent breeding colonies of Gull-billed Tern were surveyed regularly (every 3–4 days) throughout the breeding season during 1997–2000. These colonies were located in three different reservoirs: Los Canchales (CA), Sierra Brava (SB) and Orellana (OR) (see map in Sánchez-Guzmán et al. 2004). During surveys, we searched for new nests, recorded the status of previously marked nests and searched for chicks. Nests were marked individually, and clutch size, laying date and egg fate were recorded for a sample of nests in every colony (see Sánchez-Guzmán et al. 2004; Villegas et al. 2005 for details). Colony hatching success was defined as the percentage of monitored nests where one or more eggs hatched.

Newly hatched chicks were marked at first encounter with individually numbered plastic bands that were later replaced by standard aluminium rings. In the first capture, chicks were weighed (spring balance; ± 1 g), and head plus bill (digital caliper; ± 0.01 mm) and wing length (metallic stop ruler; ± 1.0 mm) were measured. The age of chicks was designated as day 0 when they were freshly hatched (chick still wet or with eggshell remains on its back). Otherwise, age was estimated from biometrics following the equation of Sánchez-Guzmán and del Viejo (1998) for this species and population: age (days) = $0.213 \times$ head plus bill + $0.097 \times$ wing length – 8.844 ($r^2 = 0.974$, $P < 0.0001$). Banded chicks were retrapped and weighed as often as possible until they died, disappeared or fledged. Chicks fledge on average when 28–35 days old; hence chicks that were at least 20 days old when last handled and not found dead thereafter were considered to have fledged.

Fledging success was defined as the percentage of banded chicks that survived to fledging.

Blood was collected from a sample of fledglings (mean age 21.1 ± 3.4 days, range 18–28 days) in each colony for molecular sexing and plasma metabolite analysis. Blood samples (150 μ l) were taken by puncture of the brachial vein with a sterile needle (26 G) and transferred to a microcentrifuge tube. The samples were kept in portable coolers at 4 °C and centrifuged (8,000 g, 10 min) within 3 h from sampling. The plasma and red blood cells were separated and stored at –20 °C for analysis at a later date.

Chick growth

We could not obtain sufficient repeated measurements to calculate complete growth curves for individual chicks, so data from individual chicks were pooled to generate an average growth curve, and chick deviation from the average growth was used to calculate a growth index for each chick (e.g. Hartley et al. 2000; Mullers and Tinbergen 2009). Data were pooled across colonies for analysis, and growth indices were calculated and tested between colonies and for sexual variation (Mullers and Tinbergen 2009).

A logistic equation of the form $M = A / \{1 + \exp[-k(t - T)]\}$, where M is body mass (g), A is asymptotic body mass (g), k is the growth constant, t is the age of the chick (days), and T is the inflection point of the curve (days; Starck and Ricklefs 1998) was used to describe the body mass growth of all fledged chicks ($n = 192$; weighed at least four times). Growth function was fitted using a least squared nonlinear regression procedure with a Levenberg–Marquardt algorithm. To calculate individual chick growth indices, for each data point we generated standardised residuals from the logistic curve, which were then averaged for each chick in three different growth periods (e.g. Arnold et al. 2006): early (0–3 days), middle (4–18 days) and late (19–25 days). Age intervals were derived from growth curves generated for captive chicks of this species (Albano et al. 2011b). The growth indices for each growth period were calculated only for chicks that had at least two weight measures within this developmental stage.

Laboratory analyses

Plasma levels of ALP, triglycerides and uric acid were assayed in a multiparameter chemistry analyser (Falcor 300; Menarini Diagnostics, Barcelona, Spain) with commercial kits (Menagent; Menarini Diagnostics) adapted to small sample volumes (Villegas et al. 2002). The analyser was calibrated with a commercial calibrator kit (Menagent; Menarini Diagnostics), and control reference serums (Menagent; Menarini Diagnostics) were run together with plasma samples. In some cases, the amount of plasma

Table 1 Breeding parameters registered in the six Gull-billed Tern colonies studied

Year	Site ^a	Laying date ^b		Clutch size			Hatching success ^c		Fledging success ^d	
		<i>n</i>	Mean ± SD	<i>n</i>	Mean ± SD	Mode	Nests hatched (%)	<i>n</i>	Chicks fledged (%)	<i>n</i>
1997	CA	150	38.5 ± 9.42 a ^e	150	2.73 ± 0.58 a ^e	3	86.5	148 a ^f	76.0	342 a, b ^f
1997	OR	59	38.9 ± 4.33 a	59	2.44 ± 0.67 b	3	82.5	57 a	65.6	122 a
1997	SB	62	35.3 ± 6.76 a	55	2.85 ± 0.44 a	3	98.2	55 a	84.3	146 b
1999	CA	295	50.3 ± 8.83 b	298	2.26 ± 0.69 c	2	84.1	296 a	43.4	399 c
2000	OR	32	80.7 ± 6.20 c	56	2.17 ± 0.69 c	2	64.8	54 b	80.0	55 a, b
2000	SB	240	48.1 ± 5.28 b	240	2.46 ± 0.75 b	3	57.2	222 c	78.5	149 a, b

Clutch size mode indicates the most frequently occurring clutch size in the colony

SD Standard deviation

^a CA Los Canchales reservoir, OR Orellana reservoir, SB Sierra Brava reservoir

^b Days from April 1

^c Percentage of monitored nests with one or more hatched eggs

^d Percentage of monitored chicks that survived to fledge

^e Different lowercase letters following a mean in a column indicate significant differences between colonies according to Tukey post hoc test ($P < 0.05$)

^f Different lowercase letters following a percentage in a column indicate significant differences between colonies by pair-wise comparisons between colonies ($P < 0.003$)

obtained was insufficient for the assay of the three metabolites so that sample sizes were not uniform.

DNA was extracted from red blood cells using Chelex (Bio-Rad, Hercules, CA), following the manufacturer's protocol. Chick sex was determined by PCR amplifications of the CHD genes following the protocol of Fridolfsson and Ellegren (1999).

Statistical analysis

We used one-way analysis of variance (ANOVA) followed by a Tukey post hoc test to assess colony (combination of year and colony site) differences in laying date (days elapsed from first day of April) and clutch size (log-transformed). Each breeding colony was assumed to be an independent group reflecting local conditions in each reservoir for a particular year and, therefore, the 'colony' effect had six levels. Hatching and fledging success were compared among colonies with the maximum-likelihood chi-square (χ^2) test followed by pairwise comparisons with the Bonferroni correction. The effect of sex and colony on chick growth indices and fledgling nutritional condition was analysed using a general linear model (GLM) with growth index or plasma metabolites as the dependent variable, respectively, and sex, colony and the interaction term as fixed factors. We controlled for the potential effect of chick age and time of sampling in plasma metabolites by including them as covariates in the models. Metabolite data were log-transformed to achieve normality. Due to the small sample size for growth data and blood samples from complete broods, we restricted the analyses to data of one

randomly selected chick per brood to avoid pseudoreplication caused by the non-independence of chicks within a nest, provided that siblings had at least two weight measures within a developmental stage. All analyses were performed using Statistica software ver. 7.0 (StatSoft, Tulsa, OK), and the level of significance was set at $P < 0.05$.

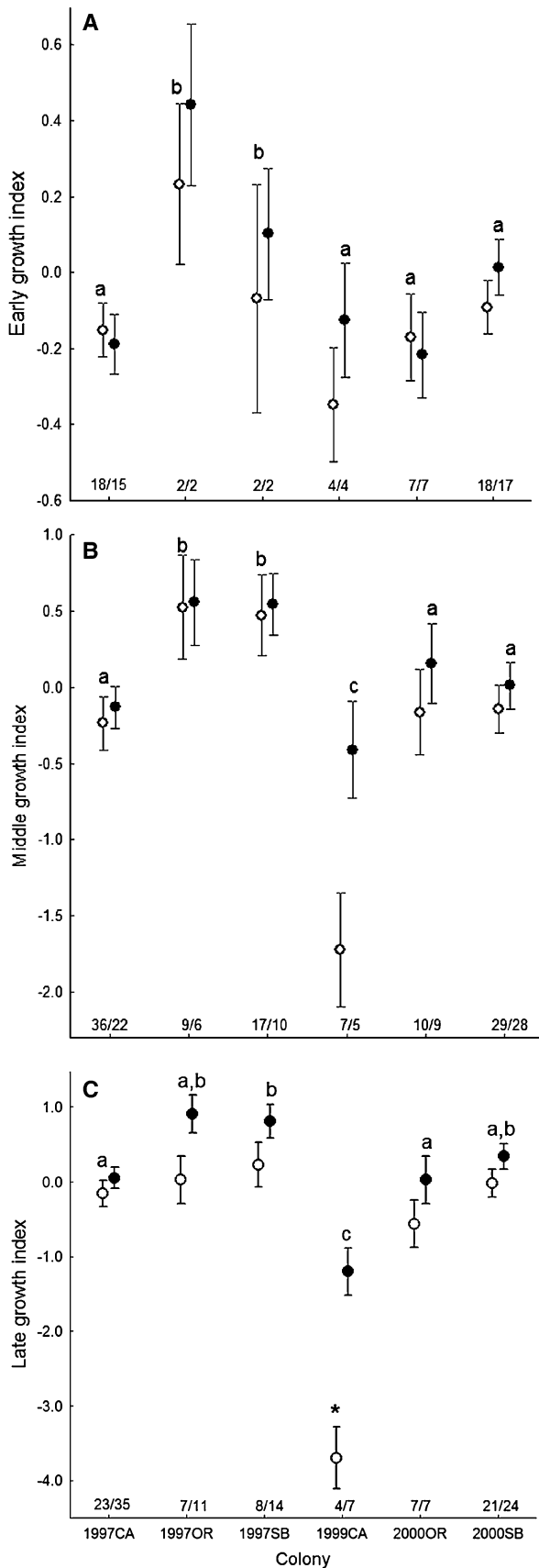
Results

Colony breeding parameters

Studied colonies differed in laying dates ($F_{5,838} = 190.10$, $P < 0.001$) and clutch size ($F_{5,858} = 15.37$, $P < 0.0001$). Birds laid earlier and laid larger clutches in the three colonies of 1997 than in those of 1999 and 2000 (Table 1). In 2000, the colony located in OR showed a considerable delay in egg-laying (Table 1). Both hatching ($\chi^2 = 160.8$, $df = 5$, $P < 0.001$) and fledging success ($\chi^2 = 142.7$, $df = 5$, $P < 0.001$) showed significant differences among colonies. The lowest hatching success was registered in the two colonies monitored in the year 2000 (Table 1), while fledging success was lower in the colony of CA in 1999 (hereafter 1999CA) than in the remaining colonies (43.4 vs. 78.9 ± 0.1 % chicks fledged; Table 1).

Chick growth and fledgling condition

The body mass gain of chicks during the early period of growth differed significantly among colonies, but was similar for males and females (Colony: $F_{5,91} = 3.19$, $P = 0.01$;



◀ **Fig. 1** Variation in early (a), middle (b) and late mass (c) growth indices [mean ± standard error (SE)] of male (solid circles) and female (open circles) Gull-billed Tern chicks in the studied colonies. Colonies are denoted by the sampling year (1997, 1999, 2000) followed by the abbreviation of the colony location (CA Los Canchales reservoir, OR Orellana reservoir, SB Sierra Brava reservoir). Sample size (number of female/male chicks per colony) is indicated at the bottom of the graph, above the x axis. Differences between colonies with the same letter in common are not significant. Significant differences between sexes within a given colony are identified with an asterisk (Tukey's post hoc test, $P < 0.05$)

Sex: $F_{1,91} = 0.72$, $P = 0.40$). During this phase, chicks were heavier in the colonies located in the OR and SB reservoirs in 1997 than in the remaining colony (Fig. 1a).

Both colony and sex had a significant effect on the growth indices of chicks during the middle (Colony: $F_{5,176} = 7.45$, $P < 0.001$; Sex: $F_{1,176} = 5.07$, $P = 0.02$) and late (Colony: $F_{5,156} = 20.77$, $P < 0.001$; Sex: $F_{1,156} = 29.53$, $P < 0.001$) phases of growth. The highest values of both indices of nestling growth were recorded again in the colonies of the OR and SB reservoirs in 1997 and the lowest in colony 1999CA (Fig. 1b, c). While males gained more mass than females between 4 and 18 days of age (Fig. 1b), the interaction colony × sex was significant between 19 and 25 days of age (colony × sex: $F_{5,156} = 3.49$, $P < 0.01$), indicating that the effect of colony in pre-fledging mass was different for male and female chicks. Pre-fledging females did catch up to males, and both sexes had a similar late growth index in all but colony 1999CA, where females maintained a significantly lower growth compared to males (Tukey post hoc test $P < 0.01$; Fig. 1c).

With regard to fledgling physiological condition, both ALP and plasma triglyceride levels differed among colonies (Table 2). Chicks in the 1997 colonies showed the highest plasma triglyceride concentration and the lowest plasma ALP level (Fig. 2). Whereas no sex or sex × colony effect was evident in plasma ALP (Table 2), plasma triglycerides differed between sexes, and there was a significant interaction between colony and sex for this metabolite (Table 2). A post hoc test revealed that females in the 1999CA colony had lower plasma triglyceride levels than males, while this metabolite being similar in both sexes for the other colonies (Fig. 2a). Neither colony nor sex had a significant effect on plasma uric acid levels (Table 2).

Discussion

The Gull-billed Tern colonies studied showed variation in breeding performance. Overall, birds laid earlier, laid larger clutches and had higher breeding success in the three

Table 2 Results of general linear models testing the effects of colony, sex and their interaction on plasma metabolite levels of Gull-billed Tern chicks

Variable	ALP			Uric acid			Triglycerides		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Colony	20.67	5,154	<0.001	2.04	5,162	0.078	6.04	5,161	<0.001
Sex	1.34	1,154	0.249	1.08	1,162	0.299	4.13	1,161	0.043
Colony × sex	1.35	5,154	0.245	0.90	5,162	0.476	2.57	5,161	0.029
Age	12.59	1,154	<0.001	0.39	1,162	0.531	0.83	5,161	0.364
Sampling time	4.23	1,154	0.04	3.25	1,162	0.073	1.59	5,161	0.209

Bold values are statistically significant

ALP Plasma alkaline phosphatase

colonies of 1997. The considerable delay in egg-laying found in the colony located in the OR reservoir in 2000 was probably a consequence of being a replacement colony formed by individuals from another colony site that abandoned their first clutches due to the predation pressure of a nocturnal raptor (own unpublished data). On the other hand, colony 1999CA showed one of the latest mean egg-laying dates and smallest clutch sizes, excluding the re-nesting colony, and the lowest fledging success registered in any of the studied colonies.

Breeding parameters, such as laying date, clutch and egg size or breeding success can reflect the environmental or parental conditions at the time of breeding (e.g. González-Solís et al. 2005; Paillisson et al. 2007; Dänhardt and Becker 2011). Therefore, observed differences for these parameters among Gull-billed Tern colonies indicate that either the parental quality or the environmental conditions differed among them, being worse in the 1999CA colony than in the remaining colonies. Inter-colony differences in chick performance point in the same direction. In the 1999CA colony, chicks of both sexes grew more slowly and fledged in a worse nutritional condition, as indicated by their lower late growth index and plasma triglyceride levels, than those of the other the colonies.

The vulnerability of Gull-billed Tern chicks to poor breeding conditions in the studied colonies varied in relation to their sex, as shown by the within-colony differences between males and females in fledgling condition observed in the 1999CA colony. In this colony, pre-fledging males had both a higher growth index and a better nutritional status than females. Thus, although these results must be interpreted with caution given the small sample size for the 1999CA colony, the negative impact of growing in a harsh environment on Gull-billed Tern chicks appeared to be, contrary to our expectations, more pronounced for females than for males.

These results are consistent with the results of a number of recent studies examining sex differences in nestling environmental sensitivity in bird species with no or negligible sexual size dimorphism. These studies found that the

adverse effects of poor rearing conditions, such as experimentally decreased maternal provisioning (Rowland et al. 2007), experimentally enlarged broods (Råberg et al. 2005; but see Saino et al. 2008; Rosivall et al. 2010), or being the last hatched chick within a brood (Oddie 2000, Becker and Wink 2003; but see Fletcher and Hamer 2004), were more acute in female than in male chicks.

Chick growth rate and fledgling mass are considered to be sensitive indicators of local environmental conditions (e.g. Lake et al. 2008; Dänhardt and Becker 2011; Lyons and Roby 2011), and a range of environmental factors have been identified as determinants of both parameters (Dmitriev 2011). Alternatively, plasma metabolite profiles have proven to be useful indicators of physiological condition in free-living birds (e.g. Ardia 2006; Norte et al. 2009; Albano et al. 2011a; Bauch et al. 2010). Specifically, triglycerides are the predominant form of energy storage in birds, nestlings included (Ardia 2005); their plasma levels increase when dietary fat is transported to adipose tissues and energy-consuming organs (Williams et al. 1999) and have been found to be positively related to individual quality and body condition in nestlings (Masello and Quillfeldt 2004; Rodríguez et al. 2011).

Moreover, in spite of being among the older chicks when blood was sampled (mean age 24.0 ± 0.9 days), fledglings in the 1999CA colony had one of the highest levels of plasma ALP activity, suggesting a delayed completion of bone mineralisation (Tilgar et al. 2008). This response has also been described in other species under unfavourable rearing conditions (Viñuela and Ferrer 1997; Tilgar et al. 2004; but see Robinson et al. 2002).

The greater vulnerability of female Gull-billed Tern fledglings when rearing conditions deteriorate could be explained by a disadvantage, due to their smaller size, in scramble sibling competition for the limited food provided by the parents. Hatching asynchrony occurs in Common Terns; therefore, larger first hatched chicks are more likely to reach the parent more quickly than their younger siblings and consequently monopolise the single prey item

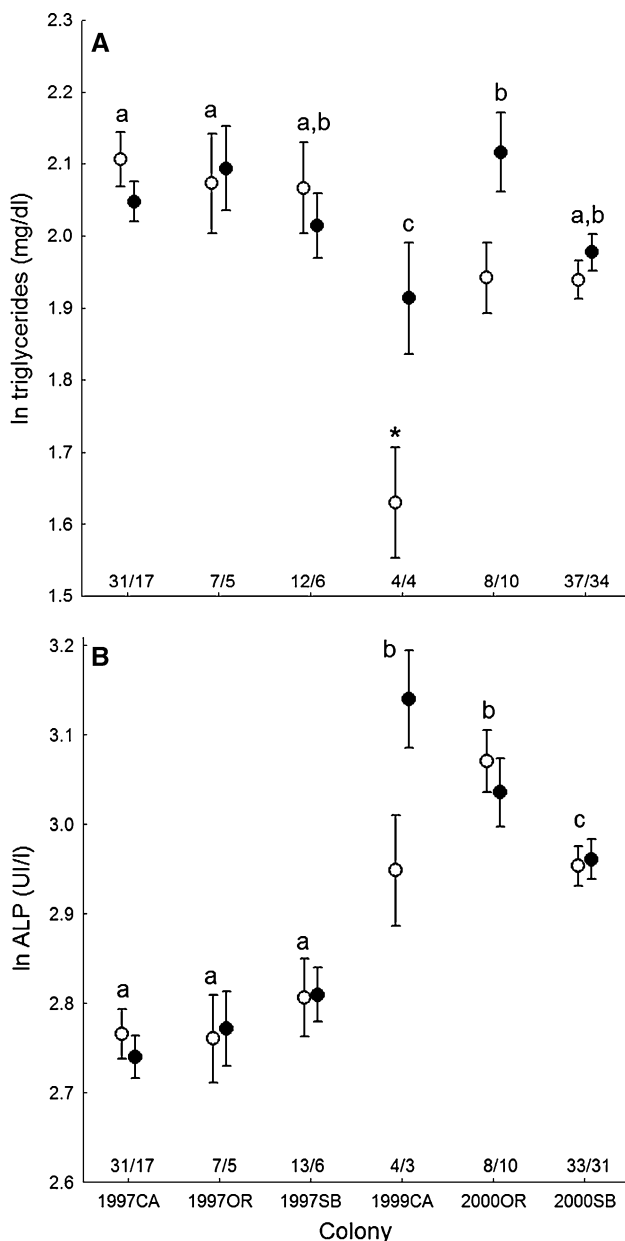


Fig. 2 Variation in plasma levels of plasma triglycerides (**a**; mean \pm SE) and alkaline phosphatase (ALP; **b**; least-square mean \pm SE) of male (*solid circles*) and female (*open circles*) Gull-billed Tern chicks in the study colonies. Colonies are designated as in Fig. 1. Sample size (number of female/male chicks per colony) is indicated at the bottom of the graph, above the x axis. Differences between colonies with the same letter in common are not significant. Significant differences between sexes within a given colony are identified with an asterisk (Tukey's post hoc test, $P < 0.05$)

supplied. This advantage appears to be a result of their ability to outrun their younger siblings owing to their larger size (Smith et al. 2005). Small sexual differences in growth and size in this species may not result in considerable disparity in energy requirements, but even a small size advantage can be beneficial in sibling competition when food is scarce (Uller 2006).

In their study on Common Terns (*Sterna hirundo*) in which they compared the condition of male and female last hatched chicks (which are more likely to receive less parental care), Becker and Wink (2003) found that sons reached a higher peak mass and fledged heavier than daughters. However, sex-specific survival was not measured in their study nor in our study. Two other studies have compared sex-specific chick survival according to brood size and hatching order in Common Terns; the respective authors reported a significantly lower fledging survival among males hatched in the last position (Fletcher and Hamer 2004) and from two-chick broods (González-Solís et al. 2005), suggesting a higher vulnerability of males to adverse conditions, but fledgling condition of the surviving chicks was not measured according to sex.

Both the sex-specific asymmetry in competitive ability and the differential survival prospects for achieving fledging in male and female chicks, as found in tern species, could be mediated by hormonal differences between sexes (Navara and Mendonca 2008; Braasch et al. 2011). Both higher endogenous and differential exposure to maternally derived androgens of males has been suggested as enhancing their competitive ability and may result in monopolizing food provided by their parents (Grootuis and Ros 2005), especially under harsh conditions (Oddie 2000). On the other hand, the negative effects of androgens, such as testosterone, on male immune function (Owen-Ashley et al. 2004) could result in higher risk of disease and early mortality of males (Sockman and Schwabl 2000; Müller et al. 2005; but see Bize et al. 2005). The extent of such hormonal effects may be influenced by factors such as brood size (Råberg et al. 2005), hatching order and brood sex composition (Saino et al. 2008; Braasch et al. 2011) or parasite exposure (Tschirren et al. 2003) and could be mediated by a sex-specific maternal allocation of egg components (e.g. antibodies, antioxidants) that confer passive protection to hatchlings and can influence their posterior phenotypic development (e.g. Soma et al. 2007; Martyka et al. 2011, Saino et al. 2011).

In summary, our results add to existing evidence that, even in species with no or slight sexual size dimorphism, the environmental sensitivity of nestlings during development may vary in a sex-specific way, making the reproductive value of sons and daughters and the fitness consequences of sex-specific resource allocation and brood sex ratio manipulation differ according to parental or environmental conditions at the time of breeding.

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