

FLEDGLING SEX RATIO VARIATION IN COLONIES OF GULL-BILLED TERN *GELOCHELIDON NILOTICA*

PATRONES DE VARIACIÓN EN LA RAZÓN DE SEXOS AL VUELO EN COLONIAS DE PAGAZA PICONEGRA *GELOCHELIDON NILOTICA*

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Fisher (1930) predicted that natural selection should favour equal parental investment in male and female offspring, and that population sex ratios at the end of the period of parental care should be inversely related to the cost of producing individuals of each sex if fitness returns from investment in sons and daughters are similar. However, when the relationship between fitness return and environmental conditions differs between sexes, natural selection would favour facultative adjustments of offspring sex ratio in response to varying environmental conditions at the time of breeding (Trivers & Willard, 1973; Charnov, 1982).

There is growing empirical evidence that birds are able to manipulate the sex of their offspring and that this manipulation can be adaptive (Sheldon, 1998). Offspring sex ratios have been found to vary with parental attributes, such as timing of breeding, sequence in the clutch, maternal age, and body condition (e.g. Tella *et al.*, 1996; Nager *et al.*, 2000; Szczys *et al.*, 2001; Velando *et al.*, 2002; Genovart *et al.*, 2003), and with environmental conditions, such as food availability (Cooch *et al.*, 1997; Torres & Drummond, 1999).

In Terns, a family of birds with negligible sexual size dimorphism, recent studies have found sex-specific differences in nestling mor-

tality (Szczys *et al.*, 2001; Fletcher & Hamer, 2004) and body mass growth (Becker & Wink, 2003), and have reported biases in hatching and fledgling sex ratio (Szczys *et al.*, 2001; Fletcher & Hamer, 2004), suggesting that, even in species without strong sexual dimorphism, sons might be more expensive to rear than daughters or more vulnerable to adverse conditions during growth.

This paper reports the patterns of fledgling sex ratio variation in different colonies of Gull-billed Tern *Gelochelidon nilotica*, a monogamous tern with adult males approximately 4% larger than females (Sánchez & Fasola, 2002).

Data were collected during 1997, 1999, and 2000 in six colonies of Gull-billed Tern in Extremadura (SW Spain). The species has bred regularly in the region during the last decade on islets located in the large reservoirs constructed to provide irrigation for agriculture (Sánchez & Sánchez, 1991). The total breeding population of the species in the area is currently estimated at 1100 pairs (Sánchez, 2003). Colonies included in this study were located in three different reservoirs, Los Canchales (1997, 1999), Sierra Brava (1997, 2000), and Orellana (1997, 2000). Regular surveys of the colonies were performed during the breeding season in order to study the numbers and reproductive performance of the birds. Nests and eggs were marked,

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and the clutch size and laying date were recorded for most nests in each colony. Newly hatched chicks were identified with individually numbered plastic bands when first found, and were later ringed with numbered metallic rings (Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente, Spain). Chicks were searched for in each visit to the colony until they disappeared or fledged.

The mean clutch size of the colonies was used as an index of the parental or environmental situation of the colonies during the breeding season. Data recording began some time after the start of incubation in some colonies. Thus the original clutch size of some nests might have been underestimated if there were losses by predation before the start of monitoring. Egg predation rates in the colonies studied were low (0.7 - 2.5%), with no statistically significant differences between them ($\chi^2 = 8.51$, $df = 5$, $P = 0.13$), and therefore the bias, if any, would be expected to be small.

A sample of chicks was blood-sampled in each colony each year when they were approximately 20 days old. Blood (*ca.* 50 μ l) was taken from the brachial vein, transferred into a tube with 1 ml of 100% ethanol and stored at 4°C until analysis. Sex was determined using polymerase chain reaction (PCR) amplifications of the CHD genes (Ellegren, 1996), with the modified protocols of Fridolfsson & Ellegren (1999).

Differences in laying dates and clutch sizes between colonies were tested with one-way ANOVA and Kruskal-Wallis tests, respectively, with subsequent Tukey and Nemenyi post-hoc tests for multiple comparisons (Zar, 1999). The sex ratio was defined as the proportion of males in the sample of sexed chicks. A G-test was used to examine departures from 1:1 in the fledgling sex ratio, and a logistic regression analysis to study the effect of colony site, year, mean laying date, and mean clutch size on the fledgling sex ratio of the colonies.

The mean clutch size of the colonies studied ranged from 2.17 to 2.73 eggs per nest and

the mean laying date between the beginning of May and the middle of June. Both variables showed significant differences between colonies (clutch size: Kruskal-Wallis test: $\chi^2 = 76.55$, $df = 5$, $P < 0.001$; ANOVA: laying date: $F_{5,1049} = 92.32$, $P < 0.001$). Birds breeding in Los Canchales and Sierra Brava in 1997 laid earlier and had larger clutches than those breeding in the other colonies (Table 1).

A total of 460 fledglings were sexed in the six Gull-billed Tern colonies. The proportion of fledgling males varied significantly between colonies ($G = 11.12$, $df = 5$, $P = 0.048$), and two of them, Los Canchales and Sierra Brava in 1997, showed a significant bias towards males, with sex ratios of 62% and 69%, respectively (Table 1). The logistic regression indicated no significant dependence of sex ratio on colony site, year, or mean laying date ($P > 0.05$). Only mean clutch size had a significant effect on the proportion of fledgling males (Wald: $\chi^2 = 6.81$, $df = 1$, $P = 0.009$).

Breeding parameters, such as laying date, clutch and egg size, or hatching, and fledgling success can reflect the environmental or parental situation at the time of breeding (*e.g.* Sydeman *et al.*, 1991; Suddaby & Ratcliffe, 1997; Oro *et al.*, 1999), and therefore comparisons of these variables between colonies may signal differential breeding conditions in them. Since reproduction is a costly process that involves an investment of effort that can impair parental condition and survival, parents should adapt the number of chicks to their rearing capacities under the specific breeding conditions (Stearns, 1992), and the first way to do this is by modifying the clutch size (Murphy, 2000). A relationship between clutch size and food availability, female age, or female body condition has been found in several tern species (*e.g.* Safina *et al.*, 1988; Suddaby & Ratcliffe, 1997; Fletcher & Hamer, 2004). Thus, the inter-colony differences in the mean clutch size of Gull-billed Tern in the present study suggest differences

TABLE 1

Fledgling sex ratios and breeding parameters in the Gull-billed Tern colonies studied.

[Razón de sexos al vuelo y parámetros reproductores en las colonias de Pagaza Piconegra estudiadas.]

| Year | Site ⁽¹⁾ | Clutch size [Tamaño de puesta] | | Laying date ⁽²⁾ [Fecha de puesta] | | Fledgling sex ratio [Razón de sexos de volantones] | | | |
|------|---------------------|-----------------------------------|-----|-------------------------------------------------|-----|-------------------------------------------------------|-----|------------------|-------|
| | | Mean ± SD | n | Mean ± SD | n | % Males | n | G ⁽³⁾ | p |
| 1997 | CA | 2.73 ± 0.58 ^{A(4)} | 158 | 5.9 ± 1.55 ^{A(4)} | 157 | 62 | 127 | 7.63 | 0.006 |
| 1997 | OR | 2.28 ± 0.73 ^B | 144 | 8.1 ± 2.07 ^B | 141 | 50 | 26 | 0.00 | 1.00 |
| 1997 | SB | 2.63 ± 0.74 ^A | 78 | 6.35 ± 1.60 ^A | 78 | 70 | 59 | 9.19 | 0.002 |
| 1999 | CA | 2.23 ± 0.69 ^B | 303 | 7.91 ± 1.30 ^B | 300 | 43 | 60 | 1.05 | 0.30 |
| 2000 | OR | 2.17 ± 0.69 ^B | 56 | 11.84 ± 0.99 ^C | 32 | 48 | 25 | 0.00 | 1.000 |
| 2000 | SB | 2.27 ± 0.79 ^B | 410 | 8.75 ± 2.31 ^B | 342 | 56 | 163 | 2.70 | 0.10 |

¹ CA: Los Canchales; OR: Orellana; SB: Sierra Brava. ² Weeks since 1 April. ³ G-test; df = 1 in all test, Yates' correction for continuity was used. ⁴ Different letters within a column indicate significant differences between colonies according to post-hoc tests.

in either the parental quality or the environmental conditions experienced by the individuals in them.

The fledgling sex ratio showed a clear relationship with colony breeding conditions, a greater proportion of males being produced in the colonies with greater mean clutch size. Biases in fledgling sex ratio may be due to either of two processes - the adaptive adjustment by the parents of the offspring sex ratio in favour of the sex with the higher fitness return (Trivers & Willard, 1973), or the differential pre-fledgling survival of the two sexes (Torres & Drummond, 1999; Nager *et al.*, 2000). The pattern of sex ratio variation found in the present Gull-billed Tern colonies may be due to several non-mutually-exclusive causes: (1) breeding conditions affect the fitness return and/or pre-fledgling survival more strongly in males than in females, and this causes a higher production of males under favourable breeding conditions or a higher mortality rate of males when these conditions deteriorate (Cooch *et al.*, 1997; Torres & Drummond, 1999; Fletcher & Hammer, 2004); (2) production of males varies according to position in the laying se-

quence (Velando *et al.*, 2002; Genovart *et al.*, 2003; Fletcher & Hamer, 2004), and as a consequence colonies with different clutch sizes have different sex ratios; (3) there is a seasonal decrease in the proportion of males per brood (Tella *et al.*, 1996; Velando *et al.*, 2002; Genovart *et al.*, 2003), and since early clutches are larger than late ones (Eyler *et al.*, 1999), earlier colonies have higher mean clutch sizes and sex ratios than later ones. Further studies that would include data on hatchling sex ratios and patterns of sex-linked pre-fledgling mortality are needed to fully understand how the variations in sex ratio of this species are related to the cited factors.

RESUMEN.—Este estudio presenta los patrones de variación en la proporción de sexos al vuelo en seis colonias de Pagaza Piconegra *Gelochelidon nilotica* de Extremadura (SO España), en relación con las condiciones reproductoras de las mismas. La proporción de sexos varió entre colonias, encontrándose un mayor número de machos en las colonias con un tamaño medio de puesta ma-

yor. Factores como la existencia de diferencias en la producción o supervivencia de machos y hembras en función de las condiciones ambientales o parentales, de la fecha de puesta o del orden dentro de ésta, pueden ser la causa de esta variación, aunque son necesarios más datos para determinar de forma precisa los patrones de variación en la proporción de sexos de esta especie.

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