

Variability in breeding parameters of the Squacco Heron *Ardeola ralloides*

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Capsule Breeding parameters and body condition of chicks varied with colony sites.

Aims To investigate variations of breeding parameters and chick body condition.

Methods In 2000, marked nests ($n = 86$) were surveyed weekly at four colonies and each nestling was measured and weighed. Nest survival probabilities during the egg and nestling periods were estimated, and the number of fledglings per breeding attempt were estimated and compared between colonies.

Results The mean clutch size of all colonies combined was four eggs but varied significantly (Kruskal–Wallis = 10.4, $P = 0.01$) between colonies. Daily nest survival probabilities during the egg and nestling periods were constant across colonies and were $0.983 (\pm 0.005 \text{ se})$ and $0.999 (\pm 0.009 \text{ se})$, respectively. Nest survival during the entire breeding period was 0.7. The number of fledglings per breeding attempt was $1.8 (\pm 0.02 \text{ se})$ and varied between colonies. The body condition of chicks varied with colony site and size rank of chicks in the brood hierarchy, i.e. the first hatched having a better condition.

Conclusions The differences between colonies were mostly in laying date, clutch size, number of fledglings per breeding attempt and chick condition. We conclude that breeding parameters need to be monitored over several breeding colonies in order to obtain reliable estimates.

The Squacco Heron *Ardeola ralloides* is considered to be vulnerable throughout its European breeding range. The largest populations occur in eastern Europe where the most serious declines have been reported (Tucker & Heath 1994). In the western Mediterranean, numbers have fluctuated with some populations showing a slight increase (Heath & Evans 2000, Kushlan & Hafner 2000). However, breeding populations are small and susceptible to catastrophic events (Hafner *et al.* 2001). In the Mediterranean region the greatest threat is the loss and deterioration of freshwater feeding and breeding habitat (Tucker & Heath 1994, Hafner & Didner 1997).

During the past 20 years the breeding biology of colonial herons in Europe has been the subject of many studies and for most species there is a considerable body of data (see Kushlan & Hafner 2000). The Squacco Heron is the least known with few published data on breeding biology (Sterbetz 1960–61, Voisin 1991, González-Martín 1994, Hafner & Didner 1997, Hafner *et al.* 2001).

As long-term data on breeding parameters has

revealed a considerable decline in clutch size, and hence, brood size (Hafner *et al.* 2001) there is concern for the Squacco Heron in the Camargue, a wetland complex which holds 80–90% of the total French population. Here, we tested whether breeding parameters (clutch size, brood size, etc.) varied between colony site at four colonies studied in 2000. We estimated nest survival probabilities during egg and nestling periods, the number of fledglings per breeding attempt and a body condition index for the chicks.

METHODS

Study area and data collection

In the Rhône Delta (43°30'N, 4°30'E) Squacco Heron nest in mixed-species colonies with Little Egrets *Egretta garzetta*, Cattle Egrets *Bubulcus ibis*, Black-crowned Night Herons *Nycticorax nycticorax* and Grey Herons *Ardea cinerea*. The study area is a mosaic of freshwater marshes, rice fields, halophyte vegetation and saline lagoons; although the Squacco Heron feeds almost exclusively in freshwater habitats including rice fields (Fasola 1994).

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Field studies at four colonies lasted from mid-April through July 2000. The Redon 1 (RED1) and Redon 2 (RED2) colonies were situated in Tamarisk trees *Tamarix gallica* and were surrounded by water at the north and by sansouires at the south. The Grand Mar (GMAR) colony was situated in Elm trees *Ulmus campestris* along a freshwater canal surrounded by reedbeds (*Phragmites australis*). The Musette (MUS) colony was situated in a wood of Ash trees *Fraxinus* sp. surrounded by water, reedbeds and rice fields. Each colony was surveyed weekly for nests, which were marked and checked on subsequent visits. Most nests were directly examined, all others were observable using a mirror pole.

In order to estimate breeding chronology, timing of breeding was back-calculated using the tarsus-length of the oldest chick per nest in comparison with control birds of known age, and a mean incubation time of 23 days (Sterbetz 1960–61, Hafner unpubl. data). Although these data are not very accurate, they provide a reasonable estimate of the chronology in time of nest establishment. Analysis followed Hafner (1977) and Prosper & Hafner (1996), dividing the breeding season into ten-day periods; e.g. period one was 1–10 May.

We recorded final clutch size and the number of chicks at last check, i.e. brood size when chicks were aged 15–20 days (about 20 days before fledging). The chick/egg ratio was defined as the proportion of eggs hatching in nests where the whole nest did not fail; i.e. brood size/clutch size. This ratio incorporates the early losses (between hatching and last check) and hatching success (the proportion of eggs in the clutch which hatch successfully). The chick/egg ratio may be slightly overestimated because chicks may stay in the nest until 30 days (Hafner & Didner 1997) and we were not able to estimate losses after about 20 days.

Nestlings (full broods) were captured, measured and ringed for individual recognition as part of an ongoing survival study in the Camargue. During each visit, each nestling was measured as follows: tarsus-length from the middle of midtarsal joint to distal end of tarso-metatarsus, and body mass. All measurements were taken in millimetres to the nearest 0.5 mm, and body mass was measured with a hand-held 500 g Pesola balance to the nearest 2.5 g. A body condition index (BCI) was determined by correlating the body mass with the tarsus-length and comparing the observed body mass to that predicted by a linear regression equation (Jakob *et al.* 1996, Green 2001). The predicted body mass was calculated as equal to $a + b \times \text{tarsus-}$

length, where a and b are the intercept and slope parameters, respectively. A positive value for the BCI indicates good body condition. We allocated a size rank for each chick within a brood, according to the tarsus-length, measured at the same visit (Thomas *et al.* 1999); the chick with the longest tarsus was assigned size rank 1, the second longest size was rank 2, etc.

Statistical analysis

Estimating nest survival and chick productivity

Daily nest survival probabilities before and after hatching were defined as the probabilities that a nest would survive during a 24-hour interval within the egg or nestling periods respectively. These parameters were estimated using a formulation of the Mayfield method (Mayfield 1961, 1975, Hensler 1985) implemented in program MARK (White & Burnham 1999). To estimate daily nest survival probabilities during the egg and nestling periods, data were first fitted to overall models.^a For the egg stage, the three periods were defined as 22 May – 7 June, 8–24 June, and 25 June – 12 July. For the nestling stage, the three periods were 3–18 June, 19 June – 4 July, and 5–22 July. To test the fit of these models to the data we used the deviance and its associated degrees of freedom (Aebischer 1999). Model selection followed the step-down strategy suggested by Lebreton *et al.* (1992) and was based on Akaike's information criterion taking into account sample size (AICc; Akaike 1973, Burnham & Anderson 1998).^b

We also tested for the effect of clutch size on daily nest survival probabilities during the egg stage. For each nest, clutch size was entered in our models as an individual covariate. Variation in nest survival was then modelled as a function of clutch size using AICc for model selection.

Chick productivity was estimated as the number of fledglings per breeding attempt (FPA) (Siriwardena *et al.* 2000). Differences between FPA values were tested using pairwise z -tests (Hensler 1985).^c

Body condition index

To test for the effects of brood size, chick size rank and colony site on body condition index of chicks we used the GENMOD procedure (normal distribution; identity link function and type 1 analysis; SAS Institute Inc. 1999–2000). We considered the four colony sites for this analysis, plus two additional sites for which only these parameters were measured. Body condition index was considered as a continuous dependent variable.

RESULTS

Breeding chronology

Egg-laying was spread out over five ten-day periods, from 1 May to 20 June, with the median laying date being between 11 and 20 May (period 2). Laying dates varied significantly between colonies (Kruskal–Wallis $H = 40.17$, $df = 3$, $P < 0.001$) (Table 1).

Clutch size, nest survival and fledglings per breeding attempt

The overall mean clutch size was 4.0 ± 1.0 sd eggs per nest ($n = 86$), with clutches of four (48.2% of total clutches), five (29.4%), three (16.5%), two (3.5%) and one egg (2.3%). Clutch size varied between colonies (Kruskal–Wallis = 10.4, $P = 0.015$; Table 2). The chick/egg ratio did not vary between colonies (Kruskal–Wallis = 2.87, $P = 0.412$) and was 0.673.

Although a model with a constant daily nest survival during the egg period had a relatively low AICc compared with other models, the lowest AICc model was a model where nest survival varied with time during the egg period (Table 3). Nest survival did not vary between colonies (Table 3). Estimates of daily nest survival from model $S(t_3)$ were $0.997 (\pm 0.003 \text{ se})$, $0.964 (\pm 0.013 \text{ se})$, and $0.962 (\pm 0.036 \text{ se})$, and was 0.983

Table 1. Distribution of the clutches of the Squacco Heron as a function of the laying period and the colony site, in southern France during 2000.

| Colony | Laying period | | | | |
|-----------|---------------|-----------|-----------|-----------|------------|
| | 1–10 May | 11–20 May | 21–31 May | 1–10 June | 11–20 June |
| Musette | 0 | 12 | 0 | 3 | 1 |
| Redon 1 | 9 | 7 | 0 | 0 | 1 |
| Redon 2 | 0 | 11 | 10 | 4 | 0 |
| Grand Mar | 0 | 0 | 4 | 16 | 1 |
| Total | 9 | 30 | 14 | 23 | 3 |

Table 2. Clutch size, number of chicks per nest at last check, daily nest survival probabilities during the egg and nestling periods, and number of fledglings per breeding attempt (FPA) of Squacco Heron nesting in southern France during 2000. All values are means \pm sd with the number of nests in parentheses, except for nest survival data and FPA were values are mean \pm se.

| Colony | Clutch size | Chicks at last check | Nest survival egg period | Nest survival nestling period | Number of fledglings per breeding attempt |
|-----------------------|---------------------|----------------------|--------------------------|-------------------------------|---|
| MUS | 4.0 ± 0.75 (22) | 2.8 ± 0.94 (12) | 0.991 ± 0.006 | 1.0 ± 0.0 | 1.9 ± 0.01 |
| RED1 | 4.3 ± 1.05 (19) | 2.5 ± 1.15 (20) | 0.989 ± 0.008 | 1.0 ± 0.0 | 2.0 ± 0.01 |
| RED2 | 4.1 ± 0.70 (30) | 1.7 ± 1.48 (28) | 0.972 ± 0.011 | 1.0 ± 0.0 | 1.6 ± 0.01 |
| GMAR | 3.3 ± 1.05 (15) | 2.8 ± 1.01 (22) | 0.961 ± 0.038 | 0.996 ± 0.004 | 1.7 ± 0.05 |
| All colonies combined | 4.0 ± 1.05 (86) | 2.4 ± 1.28 (82) | 0.983 ± 0.005 | 0.999 ± 0.009 | 1.8 ± 0.02 |

Table 3. Modelling daily nest survival probability during the egg and nestling periods. The selected models are indicated in bold. Clutch indicates that daily survival probability was modelled as a function of clutch size using a logit-linear relationship. No., number of parameters of the model; DEV, the model deviance.

| Model | AICc | Δ AICc | No. | DEV |
|----------------------------|--------------|---------------|----------|--------------|
| Egg period | | | | |
| $S(t_3)$ | 61.24 | 0.00 | 3 | 55.05 |
| $S(\text{clutch})$ | 63.69 | 2.15 | 2 | 59.29 |
| $S(.)$ | 65.03 | 3.79 | 1 | 63.00 |
| $S(c)$ | 67.76 | 6.52 | 4 | 59.43 |
| $S(c*t_3)$ | 68.37 | 7.13 | 9 | 48.83 |
| Nestling period | | | | |
| $S(.)$ | 14.16 | 0.00 | 1 | 12.14 |
| $S(t_3)$ | 16.87 | 2.71 | 3 | 10.73 |
| $S(c)$ | 17.38 | 3.22 | 4 | 9.14 |
| $S(c*t_3)$ | 31.01 | 16.84 | 11 | 7.35 |

(± 0.005 se) for the constant model $S(.)$. Although a model with clutch size as a covariate of daily nest survival had a greater AICc than our best model (Table 3), the slope of the logit-linear relationship between clutch size and survival was positive (slope = 0.584 ± 0.279 se). This suggested that nests with large clutches had higher survival than nest with small clutches. The lowest AICc model during the nestling period was a model where daily nest survival probability was constant (0.999 ± 0.009 se).

The mean number of fledglings per breeding attempt was 1.78, and varied between colonies (Table 2). More particularly, the FPA for the colony RED2 was smaller than the FPA estimated for the MUS and RED1 colonies (z -test = 2.60, $P = 0.009$, and z -test = 2.61, $P = 0.009$, respectively). No significant difference in FPA was found between other colonies.

Body condition index of chicks

Tarsus-length and body mass were positively ($R^2 = 0.94$, $n = 325$, $P < 0.001$) and linearly (P value for $\text{tarsus}^2 =$

0.6) related. We calculated a body condition index BCI, including all the chicks measured, as: $BCI = \text{Observed body mass} - (-58.901 + 4.561 \times \text{observed tarsus-length})$

Our results indicate variations in the BCI of the chicks with colony site ($\chi^2_5 = 18.50$, $P = 0.0025$) and chick size rank ($\chi^2_4 = 17.80$, $P = 0.0014$) (Fig. 1). Rank four chicks had the lowest BCI (-7.7 ± 2.6 se, $n = 32$) compared to rank one (1.5 ± 1.3 se, $n = 102$), rank two (2.2 ± 1.4 se, $n = 88$) and rank three (-1.45 ± 1.7 se, $n = 65$). We did not detect any effect of brood size on chicks' BCI ($P > 0.13$).

DISCUSSION

Our results indicate that the number of fledglings per breeding attempt varied between colonies. However, since nest survival during the egg and nestling periods and the chick/egg ratio were constant across colonies, this difference was mainly due to differences in clutch size. This is in contrast to Hafner *et al.* (2001) who found no variation among colonies for clutch size or brood size. This may be due to the fact that clutch size varied during the breeding period and that breeding started late in the season in one colony (GMAR). Differences in sample size may also perhaps explain the differences found between Hafner *et al.* (2001) and our study.

Using our estimates of daily nest survival during the egg and nestling periods, the overall nest survival during both periods was 0.663. However, most (*c.* 90%) of the nest mortality occurred during the egg period. If one assumes that nest survival during the entire nestling period (*c.* 45 days) is equal to our estimate obtained during the first 17 days of the nestling period, the overall nest survival during the entire breeding period is 0.644. Given this estimate the number of fledglings per breeding attempt would be 1.73 in 2000. Daily nest survival during the egg period varied with time, with higher nest survival at the start of the breeding season. This is a common finding among birds (Klomp 1970), and herons (Pratt & Winkler 1985, Moser 1986, Vessem & Draulans 1986).

We propose two non-exclusive hypotheses for the observed fluctuations of breeding parameters in respect of colony site. First, the results may be explained by density-dependent effects through nest-site competition at the intra- or inter-specific level, as intraspecific nest density (1–7 nests of Squacco Heron/100 m²) and interspecific nest density (from 6–170 heron nests/100 m²) showed important variations between colonies (Burger 1978, Bennetts *et al.* 2000, Dami unpubl. data).

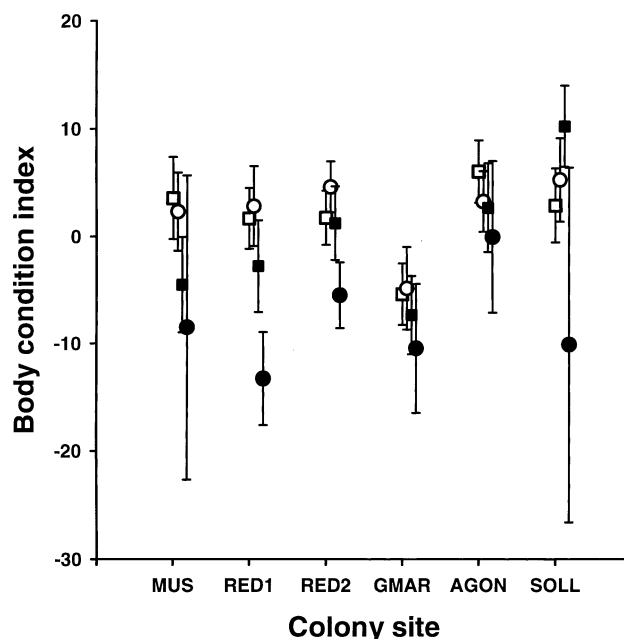


Figure 1. Body condition index (mean \pm se) of Squacco Heron chicks in relation to the size rank of the chick at each colony site in southern France in 2000. (□) chicks of size rank 1; (○) chicks of size rank 2; (■) chicks of size rank 3; (●) chicks of size rank 4.

Among the four colonies, the highest nest density was observed in GMAR which had the lowest clutch size. However, it remains to be demonstrated whether or not interspecific nest competition exists, as Squacco Herons arrive on the breeding grounds later than the other heron species.

The second hypothesis concerns the landscape around the colony. Our colony sites were mainly surrounded by mixed urbanized, cultivated and natural marsh habitats, but in different proportions (Tourenq *et al.* 2001, unpubl. data). More particularly, the GMAR colony, which had the smallest clutch size and FPA, was surrounded by a higher proportion of dry habitats (*c.* 42%) than other colonies (*c.* 13%). Since Squacco Herons feed exclusively in freshwater, this may explain part of the difference in the breeding parameters between colonies. The fact that the chicks at GMAR had the lowest body condition supports this hypothesis. As shown recently for the Little Egret, we can reasonably expect natural wetlands to remain the preferred feeding habitats for the Squacco Heron (Lombardini *et al.* 2001, Tourenq *et al.* 2001). Furthermore, studies in the Camargue on the Little Egret have shown a positive association between natural feeding habitats and brood size (Lombardini *et al.* 2001, Tourenq *et al.* 2001).

The mean clutch size of four eggs per breeding pair found in our study confirmed the significant reduction of the clutch size in the study area since the 1970s showed by Hafner *et al.* (2001). To our knowledge, Squacco Herons in southern France during 2000 had the smallest mean clutch size reported for Europe. Previous studies have found a mean clutch size of 4.6 ± 1.1 eggs in eastern Europe (Sterbetz 1960–61), and of 4.7 ± 0.7 in the Camargue in the 1970s (Hafner 1977). Similar patterns of clutch size variation have been reported for Purple Herons in the Camargue (Barbraud *et al.* 2001).

Our results indicate that there was a substantial variation of the BCI of chicks between colony sites and chick size ranks. The association between the BCI and colony site may partly reinforce the habitat quality hypothesis, although the influence of parental quality on these outcomes remains unknown (Martin 1987, Saino *et al.* 1997). However, there is little evidence of parental effects occurring among the Ardeids, and none in Squacco Heron (Cramp & Simmons 1977, Vessem & Draulans 1986, del Hoyo *et al.* 1992). Experimental studies would be needed to estimate how variation in food availability affects the body condition of chicks. The variation in BCI with respect to chick size rank may indicate that sibling competition resulted in different amounts of food being consumed by the older (and larger) chicks. This supports the current theory that the brood reduction observed in many species of Ardeids is due to food shortage (Lack 1949, Mock & Parker 1986). Variation in the body condition of the chicks may have important implications because in other bird species there seems to be a positive relationship between body mass and/or body condition of fledglings with juvenile and immature survival, and recruitment (Hochachka & Smith 1991, Williams *et al.* 1993, Perrins & McCleery 2001). Chick body condition may also influence future reproduction, as shown by Thomas *et al.* (1999) in the Little Egret.

Conservation decisions concerning endangered or vulnerable bird species are often based on data about population size or trends (Tucker & Heath 1994, IUCN Species Survival Commission 1994), although factors such as breeding parameters are important to consider. Here, we have shown that the number of fledglings per breeding attempt could vary between colonies in a relatively small study area. Thus, even at a small scale, several breeding colonies of Squacco Heron may need to be monitored to obtain reliable estimates of breeding parameters and of the body condition of the chicks.

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ENDNOTES

a. Models with time dependence with three different time periods for each colony in survival probabilities [$S(c^*t_i)$, where S is the daily survival probability, c the colony, t the period] were considered as biological starting points. We chose to use three different time periods to test for time effects on daily nest survival probabilities and to avoid over-parameterization in our modelling.

b. AICc values were used to select which model is most parsimonious in terms of providing an adequate description of the data with the smallest number of model parameters. Lower AICc values indicate 'better' models. As a general guideline, AICc values differing by > 2 are a good indication that the model with the lowest AICc value is preferable, whereas models with AICc values differing by < 2 are fairly similar in abilities to describe the data in a parsimonious manner, regardless of the magnitudes of the AICc values.

c. FPA was estimated using the following formula (after Hensler 1985): $FPA = CS \times CER \times (1 - EFR)^{EP} \times (1 - NFR)^{NP}$ where CS is clutch size, CER is chick/egg ratio, EFR and NFR are the egg and nestling period daily nest failure rate ($1 -$ daily nest survival rate), respectively, and EP and NP are the length of the egg and nestling periods in days (respectively, 23 and 17 days). The 95% confidence intervals for the estimates of fledglings per breeding attempt were calculated using an extrapolation of the formula provided by Hensler (1985). Variance estimates required for the formula were taken from the MARK output for each daily nest survival probabilities.

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