

Fluctuations in chick diet of the Squacco Heron *Ardeola ralloides* in southern France: changes over the last 30 years

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Capsule The composition varied between colony site, month and year.

Aims To determine the diet composition of chicks and its variations in 2000 and 2001. To look for any changes over the last 30 years.

Methods Chick regurgitates were analysed to determine which Order contributed most to the diet, by frequency and by biomass.

Results During 2000 and 2001 chick diet was dominated by insects (92% and 70% by biomass, respectively), mainly Coleoptera (60% and 41%) and Orthoptera (27% in both years). The dry mass of Orthoptera, Coleoptera adults, Odonata and amphibians differed significantly between breeding sites, months and years. The proportion of invertebrates (in biomass) increased from 36.5% in 1970 and 31% in 1971 to 95% in 2000 and 90% in 2001 whereas the proportion of amphibians decreased in the same time from 49% and 33% in 1970 and 1971 to 5.0% and 9.5% in 2000 and 2001, respectively.

Conclusion The proportion of prey types differed between colony sites and months. Major changes were found in the diet composition between the early 1970s and 2000s. The possible hypotheses for the observed differences are discussed.

The Squacco Heron *Ardeola ralloides* is a widely distributed species, yet it is confined to extensive freshwater areas (Hafner & Fasola 1992, Tucker & Heath 1994, Hafner & Didner 1997). Although populations were believed to be stable but fluctuating in western Europe (Tucker & Heath 1994), a recent analysis revealed a substantial long-term decline of clutch size and brood size in the Camargue, southern France (Hafner *et al.* 2001).

Food has often been reported to limit breeding performance and survival of birds (Powell 1983, Martin 1987, Newton 1998). Information on the diet of Squacco Herons concern mostly adults during breeding (Sterbetz 1960–61, Moltoni 1936, Vasvari 1938, Dementiev & Gladkov 1951), although with fewer data on the diet of nestlings (László 1986, Hafner 1977, Moser 1984, Fasola *et al.* 1993). As in other wading birds, few differences can be expected in the diet composition of adult and chick Squacco Herons

(Kushlan 1978, Telfair 1994, Fasola *et al.* 1993). No previous study has investigated diet variations between breeding sites, and over a long time period.

Here we present details of the diet composition of Squacco Heron chicks during the breeding seasons of 2000 and 2001 in the Camargue, southern France and analyse variations in diet composition in relation to breeding site, year and month. We expected dietary differences between sites, due for example to habitat heterogeneity, but also between months due to variations in prey availability. Finally, we compare these data with those obtained from the same area in 1970, 1971 and the 1980s (Hafner 1977, Moser 1984) to test for long-term trends in diet composition.

MATERIAL AND METHODS

Study area

In the Rhône river delta (43°30'N, 4°30'E) the Squacco Heron nests usually in trees in mixed colonies mostly with Little Egret *Egretta garzetta*, Cattle Egret

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Bubulcus ibis and Night Heron *Nycticorax nycticorax*. Nests are generally situated on Tamarisk *Tamarix tamarix*, elm *Ulmus* sp. and ash *Fraxinus* sp. The study area is a mosaic of shallow wetlands with four principal habitat types: saline lagoons, brackish marshes and lagoons, freshwater habitat, and rice fields (Britton & Podlejski 1981). The Squacco Heron feeds almost exclusively in freshwater habitats and rice fields (Hafner *et al.* 1982, Fasola *et al.* 1993).

Fieldwork was undertaken in 2000 and 2001 in seven of the 11 known breeding colonies of Squacco Heron: Grand Mar, Musette, Redon, Mas d'Agon, Tamaris, Sollac and Pont de Gau. These colonies hosted from seven to 67 breeding pairs of Squacco Heron.

Data collection and analysis

We monitored the breeding parameters of the Squacco Heron at their colonies from May to August of 2000 and 2001. Our presence was limited to 45 minutes per colony, in order to minimize disturbance.

All individual Squacco Heron nestlings were captured, measured and ringed. Food samples were obtained from spontaneous regurgitations of chicks. Monitoring the diet of young herons is facilitated by their propensity to regurgitate when disturbed (Kushlan 1978). This method is open to potential bias such as the differential digestion rates of each prey type, and the difference in diet of very small young from that of young near fledging (Owen 1975, Kushlan 1978, Fasola *et al.* 1993). To reduce these biases, each colony was visited early in the morning, and all regurgitates were collected from chicks 10 to 20 days old (age at ringing).

Food samples were frozen until they were placed in jars and stored in 70% alcohol for examination. Prey types found in regurgitates were identified at the species, genus or family level (Richoux *et al.* 2000) (see Appendix). Identified prey items were counted and their length measured to the nearest millimetre. Fish were measured from the tip of the snout to the fork of the tail, amphibians from snout to vent. Dry mass values for each prey type were obtained from previous research in the study area (Hafner 1977, Moser 1984, Barbraud *et al.* 2001).

We tested for the effects of month, location (breeding site), year as categorical variables and the interactions month*location, location*year and month*year on the dry biomass of the main prey type categories (in g/regurgitate) as the response variable using a generalized linear model (Poisson distribution; log link function and type 3 analysis). We considered two

locations for this analysis, Redon and Musette, for which there were sufficient diet samples ($n = 59$), during June and July of 2000 and 2001.

RESULTS

A total of 79 regurgitates (35 in 2000 and 44 in 2001), containing 2091 prey items (1177 in 2000 and 912 in 2001) were examined.

Percentage biomass

The diet of Squacco Heron chicks consisted mainly of insects which represented nearly 92% and 70% of the biomass consumed in 2000 and 2001 respectively, and fish (see Appendix, Fig. 1a). The principal prey item was *Hydrous* sp. larvae (54% and 43% of the biomass in 2000 and 2001 respectively), followed by *Gryllotalpa gryllotalpa* (25% and 38.5%) and *Cybister lateralimarginalis* larvae (5%). Fish represented an important part of total biomass (up to 19.6% for 2001) and the main species were *Cyprinus carpio*, *Pseudorasbora parva* and *Gambusia affinis* (see Appendix). Adults of genus *Rana* (4% and 4.9% of total biomass in 2000 and 2001) and *Hyla* (3.6% in 2001) comprised the majority of amphibians found in the regurgitates.

Percentage by frequency

There was a difference in the composition of chick diet between 2000 and 2001. In 2000 the majority (88%) of chick diet was made up of insects whereas in 2001 there was a shift in composition with insects comprising only 48.8% and fish increasing to 42.4% (see Appendix, Fig. 1b). The main insect species were larvae of *Hydrous* sp. (nearly 38%), *Gryllotalpa gryllotalpa* (7% in 2000 and 16.2% in 2001), *Cybister lateralimarginalis* and *Hydrochara* sp. (nearly 5% each). Mosquitofish *Gambusia affinis* (27.3% and 79.6%) and Carp *Cyprinus carpio* (28.3% and 6%) represented the principal fish species. The contribution of the amphibians varied from 1.2% to 1.9% over the same period.

Factors affecting percentage biomass

We compared the effects of month, location, year and the interactions on main prey groups. We found few statistically significant differences (see Table 1). Monthly and yearly variations were found respectively for mean dry weight of adults Coleoptera and Odonata (Fig. 2). Colony site affected the mean dry weight of

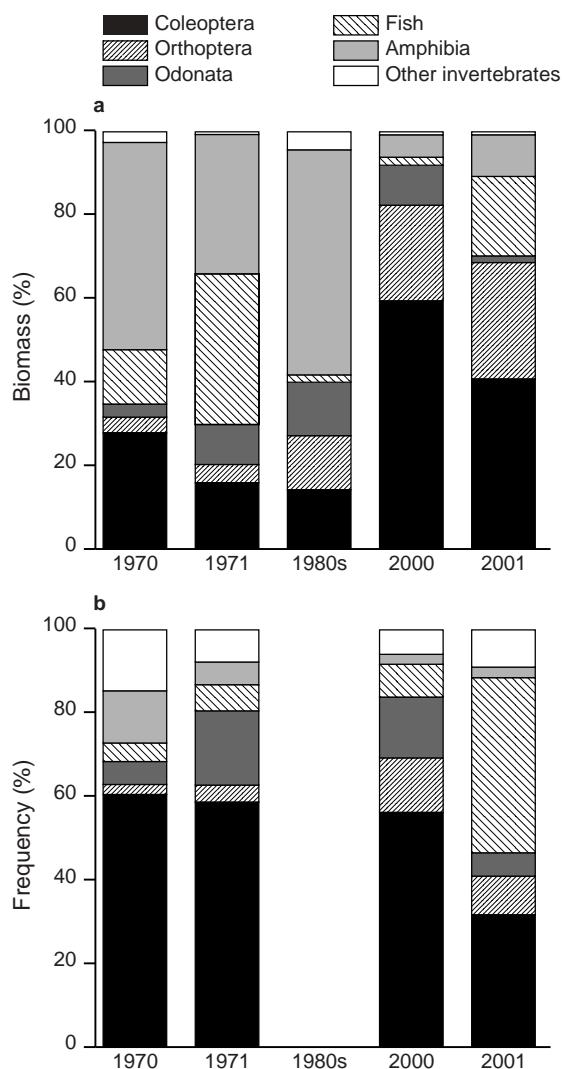


Figure 1. Percentage by (a) biomass and (b) frequency of the main prey groups consumed by Squacco Heron chicks in southern France. Data obtained from regurgitates during 1970 ($n = 335$ prey items) and 1971 ($n = 325$ prey items) (Hafner 1977), the 1980s ($n = 1346$ prey items) (Moser 1984), 2000 ($n = 1177$ prey items, this study) and 2001 ($n = 912$ prey items, this study).

adult Coleoptera, Orthoptera (Fig. 2) and other invertebrates. However, significant interactions indicated that the colony site effect varied between years for Orthoptera, and between months for the amphibians (Fig. 2).

Long-term changes in diet

The diet of Squacco Herons in the Camargue during 2000–01 in comparison with that recorded by Hafner and Moser in 1970–71 and the 1980s, showed important differences (Fig. 1) for biomass and frequency values between prey groups. The main changes were a higher percentage (in biomass) of invertebrates items in 2000–01 compared with 1970–71 and the 1980s, and an important decline in the percentage of amphibians. The observed changes in the proportion of prey types between 1970–71 and 2000–01 were confirmed if we compare the mean dry mass per regurgitate (Table 2); the mean dry mass of Coleoptera and Orthoptera increased and the mean dry mass of Amphibia and to a lesser extent of fish decreased during this period.

DISCUSSION

In this study the chicks of Squacco Heron consumed mainly invertebrates, especially insects and their larvae: terrestrial Orthoptera (crickets and grasshoppers), Dysticidae (water beetles) and Odonata (dragonflies), fish and amphibians. These results indicate that the diet of Squacco Heron chicks was broadly similar to that described in earlier studies during the breeding period in different areas (Hafner 1977, Moser 1984, László 1986, Fasola *et al.* 1993). However, no other study based on regurgitates found such a high percentage of insects in biomass, and

Table 1. Testing for the effects of month, location (breeding site) and year on the dry mass of the main prey type (in g/regurgitate) of the Squacco Heron chicks during 2000–01 in two colony sites in Camargue.

Taxon	Month	Location	Year	Location*year	Location*month	Month*year
Coleoptera						
Larvae	0.29	1.10	2.18	2.74	1.94	0.29
Adult	6.19**	14.54***	1.07	1.61	0.08	1.21
Total	0.12	0.64	2.00	2.48	1.52	0.44
Orthoptera	0.99	5.26*	2.41	4.84*	0.11	0.10
Odonata	0.00	0.72	5.31*	0.02	1.67	0.34
Other invertebrates	0.13	6.84**	0.23	1.52	3.81*	3.92*
Amphibians	0.04	0.61	2.41	0.71	4.91*	0.11
Fish	1.85	0.29	1.98	3.28	1.77	0.01

Significant *F*-values for each term of the model are in bold type. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

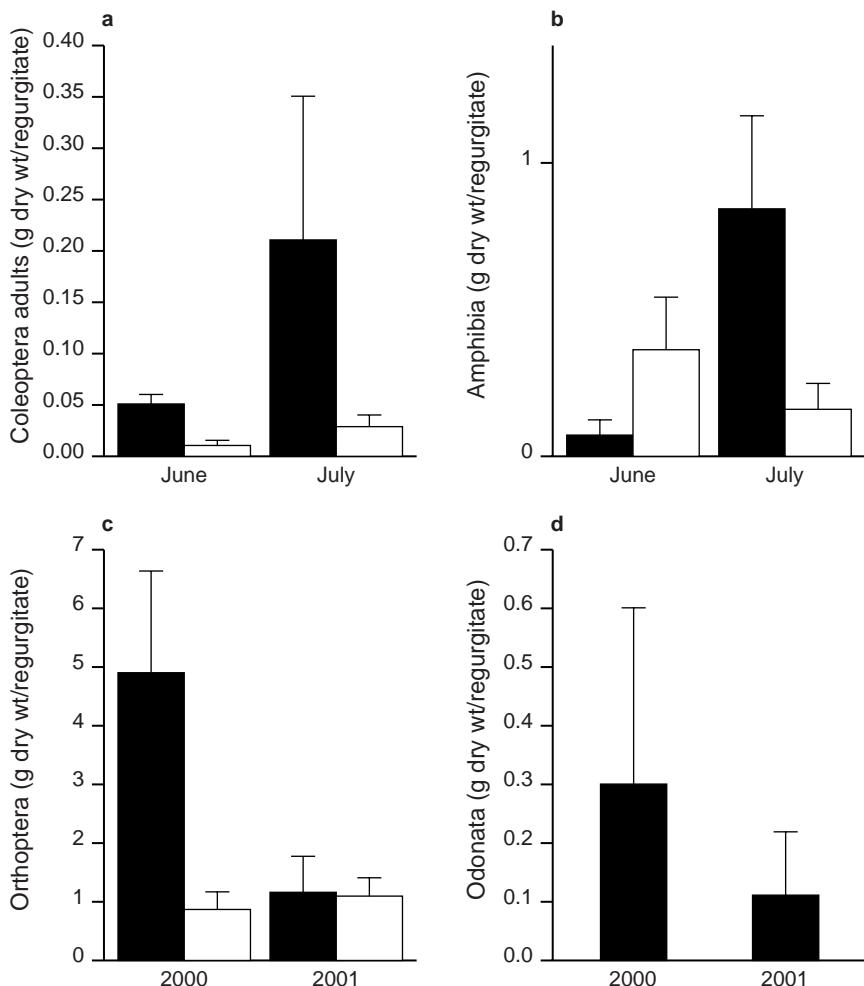


Figure 2. Mean dry weight per regurgitate (\pm se) from Squacco Heron chicks of (a) Coleoptera adults, and (b) Amphibia in June and July 2000–01, (c) Orthoptera in 2000–01 and (d) Odonata in 2000–01. Colony site in southern France: Musette (■); Redon (□).

most found a high percentage in biomass of fish and amphibians. Moreover, we found significant differences in the proportion of prey types (by biomass) consumed between colony sites and month. These differences

Table 2. Mean dry weight per regurgitate for main prey groups in the diet of Squacco Herons in southern France; data for 1970 and 1971 from Hafner (1977) and 2000 and 2001 from this study. n, number of samples.

Prey group	Mean dry weight (\pm se)			
	1970 n = 26	1971 n = 25	2000 n = 45	2001 n = 44
Coleoptera	0.89	0.52	3.01 \pm 0.62	1.58 \pm 0.30
Orthoptera	0.09	0.13	1.71 \pm 0.45	1.07 \pm 0.25
Odonata	0.11	0.29	0.30 \pm 0.08	0.11 \pm 0.02
Fish	0.43	1.17	0.25 \pm 0.11	0.76 \pm 0.16
Amphibians	1.55	1.05	0.315 \pm 0.11	0.37 \pm 0.12
Other invertebrates	0.09	0.04	0.07 \pm 0.66	0.04 \pm 0.01

probably reflect heterogeneities in foraging habitats and variability in prey life-cycles. Indeed our colony sites were surrounded by mixed urbanized, cultivated and natural habitats in different proportions (Tourenq *et al.* 2001, unpubl. data). Sterbetz (1960–61) also reported diet variations between Squacco Heron feeding in rice fields and those feeding in natural habitats.

Significant changes in the dietary composition of chick regurgitates between 1970–71 and 2000–01 were determined.

Different, though related hypotheses, may explain the observed shift in the diet from amphibians and fish to mainly insects. First, bias in analysis of food samples regurgitated by nestlings can occur due to differential digestion rates between prey groups (Owen 1975, Tigar & Osborne 2000), and regurgitates may not represent the total stomach content. However, the major differences in importance of prey groups (in percentage by biomass and in dry mass per regurgitate) between

1970–71, 1980s and 2000, 2001 suggest that changes occurred in the chick diet of the Squacco Heron in southern France. Moreover, Barbraud *et al.* (2001) found similar changes in the diet of the Purple Heron *Ardea purpurea* between the 1980s and the late 1990s within the same study area.

Second, changes in diet may be explained by changes in prey availability. Over the past 40 years, habitats within the study area have been greatly modified by human activities (extension of agriculture, salt exploitation and industry) resulting in losses of natural areas accompanied by an increase in wetlands management (Tamisier & Grillas 1994, Tourenq *et al.* 2000, Mathevet 2000). The changes in agricultural practices to increase rice production may have differentially affected prey species through variations in rice field surface area and changes in cultivation methods. Changes of irrigation practices and increased contaminant inputs (nitrate, phosphate, potassium, pesticides) may have had important direct or indirect effects on prey populations (Chauvelon *et al.* 1996, Fujioka & Lane 1997, Suhling *et al.* 2000, Berny *et al.* 2002, N. Beck unpubl. data). The water management in 'natural' habitats has changed largely due to hunting, or use for educational or conservation purposes and usually involves large inputs of freshwater. Human-induced changes in hydrology (mainly from water management) has caused important modifications on the high natural variability of water levels in the Mediterranean seasonal wetlands and may have influenced the prey community (Tamisier & Grillas 1994, Poizat & Crivelli 1997).

Finally, the changes in dietary composition of chick regurgitates between studies may also be explained by changes in the availability of prey species as interspecific competition for food resources has intensified amongst herons as their populations have increased. The number of breeding pairs of the Little Egret and of the Cattle Egret increased from 1330 and 22 in 1970–71 to 4600 and 5700 in 2000–01, respectively (Tourenq *et al.* 2000, Kayser *et al.* 2003). It has been shown that a relatively important ecological overlap in feeding habitats and diet composition exist between Squacco Heron, Little and Cattle Egret (Hafner *et al.* 1982, Bredin 1983, Moser 1984, Lombardini *et al.* 2001).

Such an important change in diet composition of Squacco Heron chicks during the breeding period raises the question of the energetic implications of such a shift. Differences in energy content per unit mass between prey groups may influence chicks' growth rates

and condition, and eventually chick survival (Cummins & Wuycheck 1971, Bell 1990, Golet *et al.* 2000). In our study area, a decrease of 0.4 chick per brood between 1970 and 1998 has been observed for the Squacco Heron (Hafner *et al.* 2001). However, the effects of these changes on the population dynamics remain unclear as the Squacco Heron breeding population shows considerable variability in numbers (Hafner *et al.* 2001).

ACKNOWLEDGEMENTS

This work is supported by Station Biologique de la Tour du Valat. The ringing programme is carried out under licence of the French National Ringing Centre (CRBPO) and the French Ministry of Environment. We thank the Conseil Général du Gard, the Centre du Scamandre and B. Blohorn and M. Dulac for permission to work on their land. We are grateful to A. Arnaud, C. Barbraud, N. Beck, P. Contournet, A. Gélin, M. Lepley, V. Lemoine, A. Dorgères and C. Tourenq for constructive discussions and assistance in the laboratory and in the field. We thank M. Fasola and an anonymous editorial assistant for useful comments on earlier drafts of this paper.

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(MS received 23 May 2002; revised MS accepted 3 June 2003)

APPENDIXDiet composition* of Squacco Heron chicks in southern France during 2000 ($n = 35$ samples) and 2001 ($n = 44$ samples).

Order	Family	Species	n		Dry weight (g)	
			2000	2001	2000	2001
Invertebrate						
Acheta			—	4	—	0.24
Gastropoda			2	—	0.02	—
Arachnida			2	54	0.04	0.61
Crustacea			25	5	1.49	0.326
Orthoptera			150	78	59.57	46.65
Odonata	Grylloidalpidae	<i>Gryllootalpa gryllootalpa</i>	73	72	51.1	45.99
Heteroptera			169	51	11.5	2.38
Coleoptera	Dytiscidae		15	13	0.15	0.31
	Hydrophilidae	<i>Cybister lateralimarginalis</i>	666	293	133.55	69.665
		<i>Hydrous</i> sp.	140	86	16.02	14.325
		<i>Hydrophilus (Hydrochara)</i>	47	27	9.44	6.345
Hymenoptera			458	202	115.09	55.27
Diptera			395	172	110.11	51.87
Vertebrate			51	20	4.36	3.07
Mammalia			32	1	0.33	0.01
Amphibia			3	9	0.12	0.37
Anura			+	—	—	—
Pisces	Rana sp.		14	17	11.161	16.121
	<i>Hyla meridionalis</i>		7	14	8.77	9.926
	Cyprinidae	<i>Cyprinus carpio</i>	1	3	0.491	6.195
		<i>Pseudorasbora parva</i>	99	387	5.75	33.27
	Poeciliidae	<i>Gambusia affinis</i>	28	23	2.64	8.83
			7	—	1.36	—
Total			27	308	0.82	17.2
			1177	912	223.681	169.952

*Only the dominant families and species are reported here. +, present; —, absent.