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Dietary Segregation of Four Ardeid Species Breeding in Anzali International Wetland, Northern Iran

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Abstract.—The nestling diets of four heron species breeding on a small forestry islet in Anzali, Iran, were investigated to determine the dietary segregation among sympatric breeders. Regurgitated samples from Black-crowned Night-Herons (*Nycticorax nycticorax*), Little Egrets (*Egretta garzetta*), Cattle Egrets (*Bubulcus ibis*) and Squacco Herons (*Ardeola ralloides*) were collected during the breeding season from 23 May to 16 August 2016. A total of 1,606 prey items were identified representing 39 prey categories from nine different classes. Differences were detected among these four ardeid species for the percentage of each prey category. Fish dominated the regurgitates of the Black-crowned Night-Heron (67%; $n = 43$ samples), Little Egret (45%; $n = 33$ samples) and Squacco Heron (53%; $n = 10$ samples), whereas arachnids and insects combined (53% and 40%, respectively, based on total number of individuals) and insects (61.9% based on weight) were the most common prey items for the Cattle Egret. Although fish items were dominant in Black-crowned Night-Herons, Little Egrets and Squacco Herons, their weight ($\chi^2_3 = 318$, $P < 0.001$) and length ($\chi^2_3 = 225.2$, $P < 0.001$) differed significantly. There was some overlap in the diet of all four heron species, especially between Black-crowned Night-Herons and Squacco Herons, with a Pianka Overlap Index equaling 0.92. There was sufficient dietary segregation in terms of number, weight and length of prey items that could contribute to a reduction in competition for limited food resources. *Received 10 April 2017, accepted 24 July 2017.*

Key words.—Anzali, Black-crowned Night-Heron, Cattle Egret, diet, Iran, Little Egret, regurgitate, Squacco Heron, wetland.

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Diet has an important role in the growth, activities and reproduction of birds (Newton 1998), and can be a significant limiting factor during the breeding period, especially for altricial species (Drent and Draen 1980; Martin 1987). Most heron species are highly dependent on wetlands, but some also feed on dry lands (Kushlan and Hancock 2005). Herons are generalist predators, capable of preying upon a wide range of taxa in relation to their availability in different habitats and regions, and thus foraging habitats of different species often overlap (Fasola *et al.* 1993; Fasola 1994). When prey is limited, resource partitioning may be one mechanism that helps reduce competition between sympatric species (Kazantzidis and Goutner 2005). However, when seasonal resources are abundant, reduced competition may lead to increased overlap (Wiens 1992). A difference in resource selection is one of the principal factors permitting the coexistence of certain species (Rosenzweig 1981). Although different species of herons vary in their habitat preferences, diet, and behavior, they have certain common fundamental requirements for nesting (Hafner 2000). The diets of various herons have been investigated across the Western Palearctic, notably in Spain (Martinez *et al.* 1992), Italy (Fasola *et al.* 1993; Fasola 1994), and Greece (Kazantzidis and Goutner 2005), but there are few studies on the diet of sympatric ardeid species in south and west Asia.

Four species of Ardeidae, the Black-crowned Night-Heron (*Nycticorax nycticorax*), Little Egret (*Egretta garzetta*), Cattle Egret (*Bubulcus ibis*) and Squacco Heron (*Ardeola ralloides*), breed in a mixed -species colony in Anzali international wetland and throughout Iran (Scott 2007; Mansoori 2008; Ashoori and Abdoos 2013). Despite the wide distribution of such heronries in Iran, there have been few studies undertaken on the breeding ecology and interactions of the species involved (Ashoori 2010; Ashoori and Barati 2013). The objective of this study was to examine prey diversity and differences in the nestling diet of these four sympatric ardeid species.

METHODS

Study Area

The study was conducted in the Anzali wetland complex (37° 25′ to 37° 30′ N, 49° 25′ to 37° 30′ E) on the southern coast of the Caspian Sea in Gilan Province, northern Iran (Ashoori and Abdoos 2013). This wetland, 19,300 ha in area, includes a mosaic of fresh and brackish water marshes, lagoons, estuaries, rivers, flood meadows and a few islets. Parts of this wetland and some of the surrounding areas are being used for rice paddy fields and aquaculture (Ashoori and Abdoos 2013). The Anzali wetland was listed as an International Wetland under the Ramsar Convention in 1975, and has subsequently been listed in the Montreaux Record due to a high level of eutrophication (Ramsar Convention 2011). This wetland is also recognized as an Important Bird Area due to its significant numbers of breeding and wintering waterbirds, including Ardeidae (Evans 1994).

Regurgitates were collected from a single mixed-species colony located in Ghalm-Goodeh (37° 27′ N, 49° 27′ E), a small (81 ha) forested islet covered predominantly with alder (*Alnus glutinosa*) and Caucasian wingnut (*Pterocarya fraxinifolia*). This islet is situated in the central part of the Anzali wetland close to the Caspian Sea. The colony size of the four heron species (Black-crowned Night-Heron, Little Egret, Cattle Egret and Squacco Heron) fluctuates annually according to changes in habitat conditions, with an average of 840 breeding pairs (Range = 600-1,100) between 2003 to 2005 and 2007 to 2008; Black-crowned Night-Herons ranged from 300-450 pairs, Little Egrets from 250-400 pairs, Cattle Egrets from 10-45 pairs and Squacco Herons from 40-205 pairs. Breeding activities by these four heron species started subsequent to other colonies in the area (Ashoori 2010; Ashoori and Barati 2013). In 2006 and 2015, the colony was abandoned, probably due to human disturbance.

Diet Sampling

The diet of herons was studied by analyzing nestling regurgitates collected during the 2016 breeding season. Regurgitates were collected weekly throughout the nestling period, from 23 May to 16 August 2016. To compare changes in the nestling diet with chick age, we used three age classes: 0-7 days (when chicks are newly hatched and the downy birds without ability to move around), 8-15 days (when chicks are able to move in the nest) and 16 days or older (chicks are able to move on adjacent branches). Each individual regurgitate sample was placed in a labeled plastic bag and transferred to the laboratory. These individual samples were then stored in formalin acid (10%) for later laboratory analyses.

Individual prey items were identified, measured and weighed. Prey items were identified to the family level since species level identification was not always possible for samples of classes such as insects and arachnids. Where prey items were complete, they were identified, measured and the wet weight recorded. Regurgitates and individual prey items were weighed to ± 0.1 g using a digital balance. In instances where the prey items were partly digested (so it was not possible to weigh the complete sample), the average weight of those items was estimated using the weight of similarly sized prey. For fish species, the total length of each item was measured ± 1 cm from the tip of the snout along the mid-line to the posterior edge of the caudal fin fold.

Statistical Analysis

To compare the median prey mass and length between the studied species, we grouped the main prey classes into fish, amphibians, insects and others, and analyzed samples using the Kruskal-Wallis χ^2 test. Also, pairwise comparison was carried out using the Mann-Whitney *U*-test. Analyses of the mass and length of prey items were performed using R software (R Development Core Team 2016) with $P < 0.05$ as the threshold of significance. The average mass of prey is reported ± SE.

Prey composition overlap among species was measured using the Pianka Overlap Index (O) (Pianka 1973) based on the numerical frequency of each prey family: where O_{ji} and O_{ki} are the proportions of the resource i used by bird species j and k, respectively. The index is symmetrical and assumes values between 0 and 1. A value of 0 suggests that the two species have no common prey, whereas a value of 1 indicates complete overlap. An overlap index > 0.6 was treated arbitrarily as a substantial overlap in the diet of two species compared (Diamond 1983; Catry *et al.* 2009; Tayefeh *et al.* 2014).

RESULTS

We collected a total of 111 regurgitates from the four heron species: Black-crowned Night-Herons ($n = 43$), Little Egrets ($n = 33$), Cattle Egrets ($n = 25$) and Squacco Herons ($n = 10$). From these, we identified a total of 1,606 prey items from nine different classes and 39 families (Table 1).

The sample size of regurgitates was small for these herons in each breeding season. For these reasons, seasonal variation in dietary composition was not analyzed. Overall, the most common prey items were insects (32.1%), Acrididae (31.4%) and fish (24.7%), and there were significant differences among heron species ($\chi^2_3 = 15.9$, $P < 0.001$, Kruskal-Wallis χ^2 test) (Table 1). The average weight of each regurgitate was 43.9 g ± 7.4 g (max = 583 g for Black-crowned Night-Heron; min = 1.5 g for Cattle Egret, $n = 111$ samples), and were 69.7 g (± 13.6

Table 1. Number of individuals (*n*) and relative abundance (RA) of prey families identified from regurgitations from the Black-crowned Night-Herons, Little Egrets, Cattle Egrets and Squacco Herons breeding in the Anzali wetland in 2016.

		Black-crowned Night-Heron		Little Egret		Cattle Egret		Squacco Heron	
Class	Family	*n*	RA (%)	*n*	RA (%)	*n*	RA (%)	*n*	RA (%)
Osteichthyes	Cyprinidae	120	58.5	86	17.1	0	0.0	28	48.3
Osteichthyes	Poeciliidae	5	2.4	119	23.6	0	0.0	0	0.0
Osteichthyes	Esocidae	4	1.9	1	0.2	0	0.0	1	1.7
Osteichthyes	Mugilidae	4	1.9	1	0.2	0	0.0	0	0.0
Osteichthyes	Cobitidae	0	0.0	15	3	0	0.0	3	5.2
Osteichthyes	Gobiidae	0	0.0	6	1.2	0	0.0	0	0.0
Osteichthyes	Atherinidae	0	0.0	1	0.2	0	0.0	0	0.0
Osteichthyes	Clupeidae	3	1.5	0	0.0	0	0.0	0	0.0
Amphibia	Ranidae	21	10.2	59	11.7	20	2.4	16	27.6
Samopsida	Colubridae	3	1.5	0	0.0	2	0.2	0	0.0
Mammalia	Muridae	1	0.5	0	0.0	0	0.0	0	0.0
Malacostraca	Palaemonidae	3	1.5	13	2.6	1	0.1	0	0.0
Malacostraca	Gammaridae	0	0.1	9	1.8	0	0.0	0	0.0
Malacostraca	Armadillidiidae	0	0.1	0	0.0	0	0.0	1	1.7
Chelicerata	Araneidae	8	3.9	43	8.5	451	53.7	0	0.0
Chelicerata	Gybaeidae	1	0.5	0	0.0	0	0.0	1	1.7
Clitellata	Piscicolidae	0	0.0	14	2.8	24	2.9	0	0.0
Diplopoda	unidentified	0	0.0	1	0.2	0	0.0	0	0.0
Insecta	Gryllotalpidae	0	0.0	2	0.4	36	4.3	1	1.7
Insecta	Agrionidae	1	0.5	8	1.6	45	5.3	1	1.7
Insecta	Acrididae	7	3.4	31	6.2	11	1.3	0	0.0
Insecta	Tettigoniidae	4	1.9	39	7.7	4	0.5	0	0.0
Insecta	Tetrigidae	0	0.0	1	0.2	0.0	0.0	0	0.0
Insecta	Gryllidae	0	0.0	21	4.2	18	2.1	0	0.0
Insecta	Noctuidae	0	0.0	0	0.0	21	2.5	0	0.0
Insecta	Tabanidae	3	1.4	2	0.4	91	10.8	0	0.0
Insecta	Carabidae	6	2.9	7	1.4	8	0.9	0	0.0
Insecta	Ricaniidae	1	0.5	0	0.0	60	7.1	0	0.0
Insecta	Corixidae	3	1.5	0	0.0	1	0.1	0	0.0
Insecta	Gerridae	1	0.5	0	0.0	1	0.1	0	0.0

Table 1. (Continued) Number of individuals (*n*) and relative abundance (RA) of prey families identified from regurgitations from the Black-crowned Night-Herons, Little Egrets, Cattle Egrets and Squacco Herons breeding in the Anzali wetland in 2016.

		Black-crowned Night-Heron		Little Egret		Cattle Egret		Squacco Heron	
Class	Family	*n*	RA (%)	*n*	RA (%)	*n*	RA (%)	*n*	RA (%)
Insecta	Dytiscidae	5	2.4	9	1.8	1	0.1	2	3.4
Insecta	Mantidae	0	0	9	1.8	0	0.0	0	0.0
Insecta	Nepidae	0	0	1	0.2	0	0.0	0	0.0
Insecta	Tipulidae	0	0	0	0.0	14	1.6	2	3.4
Insecta	Vespidae	0	0	0	0.0	1	0.1	0	0.0
Insecta	Pentatomidae	0	0	0	0.0	1	0.1	0	0.0
Insecta	Stratiomyidae	0	0	0	0.0	22	2.6	0	0.0
Insecta	Mecoptera	0	0	1	0.2	0	0.0	0	0.0
Insecta	Coloptera	0	0	0	0.0	6	0.7	0	0.0
Insecta	Lepidoptera	1	0.5	0	0.0	1	0.1	0	0.0
Insecta	unidentified	0	0	4	0.8	0	0.0	2	3.4
Total		205	100	503	100	840	100	56	100

g; n = 43 samples) in Black-crowned Night-Heron, 33.8 g (± 43.54 g; n = 33 samples) in Little Egret, 22.7 g (± 24.2 g; n = 25 samples) in Cattle Egret and 19.4 g (± 21.4 g; n = 10 samples) in Squacco Heron.

Black-crowned Night-Heron

A total of 205 prey items were identified in regurgitates of the Black-crowned Night-Heron. These regurgitates contained on average 4.8 ± 1.0 prey items (Range = 1-32, n = 43). The weight of these regurgitates ranged between 4.0 and 583.0 g, with a mean 69.7 g ± 17.4 g (from a total mass of 2,998.7 g). Fish were found in 95.3% of regurgitates, and in 25 samples (58.1%) fish were the only prey items. Fish representing five families were recorded, with Cyprinidae being the most frequent family (Table 1), followed by insects (47.6% of categories and 15.1% of prey items) and amphibians (4.5% of families and 10.2% of prey items). Reptiles, mammals, Malacostraca and arachnids were also found in low proportions (Table 1). Prey items of the Black-crowned Night-Heron weighed between 0.1 and 300.0 g with an average of 14.6 g ± 2.6 g; the mean mass of fish (20.7 g ± 2.4 g, n = 136) and prey length (11.1 cm ± 0.5, n = 136) was higher than other items (Table 2). Of the 136 fish, 108 weighed more than 7.3 g (79.4 %), and 110 (80.8%) were more than 8 cm in length (Fig. 1). The mean overall mass of reptiles, mammals and Malacostraca in the Black-crowned Night-Heron was considerable (10.6 g ± 3.3 g, Range = 3-30 g, n = 7) (Table 2).

Little Egret

For the Little Egret, we collected 503 prey items from 33 regurgitates (1,116 g mass). These regurgitates contained on average 15.2 ± 2.9 prey items (Range = 1-63, n = 33). The weight of these regurgitates ranged between 1.8 and 170.2 g, with a mean 33.8 g ± 7.6 g. Fish were found in 66.6% of regurgitates, and 27.2% of regurgitates contained only fish. Poeciliidae (52%) and Cyprinidae (37.5%) were the most common fish. The fish of seven families (24% of all families) represented the most prey items (45.5% of prey items), followed by insects (50% of families and 26.8% of prey items) and amphibians (4.1% of families and 11.7% of prey items) (Table 1).The mean fish prey length of Little Egret chicks was 4.3 cm ± 0.2 cm (Range = 0.5-15.0 cm, n = 229) (Table 2). The weight of prey ranged from 0.5 g to 50.0 g. The mean weight of insects (2.7 g ± 0.1 g, n = 135), fish (2.5 g ± 0.3 g, n = 229) and amphibians (2.3 g ± 0.1 g, n = 59) was greatest (Table 2). Of 229 fish in Little Egret regurgitates, 85.1% were less than 4.9 g, and 169 (73.7%) of items were less than 5.5 cm in length (Fig. 1).

Cattle Egret

For the Cattle Egret, we collected 841 prey items in 25 regurgitates (482.5 g mass). These regurgitates contained on average 33.6 ± 6.5 prey items (Range = 2-131, n = 25). The weight of these regurgitates ranged between 2.4 and 100.8 g, with a mean 22.7 g ± 4.8 g (64% of regurgitations contained amphibians). Araneidae (one family and 451 prey items) and insects (18 families and 343 prey items) were the most numerous prey (Table 1), but the total weight of insects (61.9% from weight; 1.1 g ± 0.06 g, Range = 0.1-4.0 g, n = 343) was considerable compared to five other classes (Table 2).

Squacco Heron

For the Squacco Heron, we collected 56 prey items in 10 regurgitates (194.5 g mass). These regurgitates contained on average 5.6 ± 2.2 prey items (Range = 1-13, n = 10). The weight of these regurgitates ranged between 1.5 and 75.3 g, with a mean of 19.5 g ± 6.7 g. Fish were found in 50% of regurgitates, and in 20% of regurgitates fish were the only prey. Cyprinidae (48.3%) and amphibians (27.6%) were the most common categories recorded (Table 1). The mean prey weight and the length of prey from Squacco Heron chicks were 3.5 g ± 1.2 g (Range = 0.1-64.0 g, n = 56) and 4.4 cm ± 0.4 cm (Range = 1.5-22.0 cm, n = 56), respectively. Fish prey length ranged between 2 and 22 cm, with a mean length of 4.7 cm ± 0.7 cm, and the

Table 2. Mean (± SE) wet weight (g) and length (cm) of dietary samples collected from Black-crowned Night-Heron, Little Egret, Cattle Egret and Squacco Heron chicks in the Anzali wetland colony in 2016.

				Weight (cm)		Length (g)	
Species	Diet	Number of Samples Present (%)	Total Number of Prey Items	Mean (± SE)	Range	Mean (± SE)	Range
Black-crowned Night-Heron	Fish	66.3	205	20.4 ± 2.4	0.3-300	11.1 ± 0.5	3-50
Little Egret	Fish	45.5	503	2.5 ± 0.3	0.1-50	4.3 ± 0.2	0.5-15
Cattle Egret	Fish	0	841	0	0	0	0
Squacco Heron	Fish	57.1	56	4.3 ± 2.2	0.1-64	4.7 ± 0.7	2-22
Black-crowned Night-Heron	Amphibian	10.2	205	4.5 ± 1.8	2-25	4.8 ± 0.3	4-8
Little Egret	Amphibian	11.7	503	2.3 ± 0.1	1-5.9	3.5 ± 0.1	2.5-5.9
Cattle Egret	Amphibian	2.4	841	5.1 ± 1.7	2-28	5.2 ± 0.5	3.5-12
Squacco Heron	Amphibian	28.5	56	2.9 ± 0.3	2-5	4.5 ± 0.3	3.5-8
Black-crowned Night-Heron	Insect	15.1	205	1.8 ± 0.2	0.2-4	2.8 ± 0.3	1-5.5
Little Egret	Insect	26.8	503	2.7 ± 0.1	0.3-4	4.0 ± 0.1	1.5-6
Cattle Egret	Insect	40.8	841	1.1 ± 0.0	0.1-4	3.9 ± 0.1	1-7
Squacco Heron	Insect	10.7	56	1.3 ± 0.4	0.4-3.3	3.5 ± 0.4	1.8-5.3
Black-crowned Night-Heron	Arachnidae	4.4	205	0.1 ± 0.0	0.1-0.2	1.0 ± 0.0	1-1
Little Egret	Arachnidae	8.5	503	0.1 ± 0.0	0.5-0.3	1.2 ± 0.0	1-2
Cattle Egret	Arachnidae	53.6	841	0.2 ± 0.0	0.1-0.3	1.5 ± 0.0	1-3
Squacco Heron	Arachnidae	1.8	56	0.2	—	1.5	—
Black-crowned Night-Heron	others	3.4	205	10.6 ± 3.3	3-30	13.4 ± 4.6	0.3-20
Little Egret	others	7.4	503	1.4 ± 0.2	0.5-3.5	4.8 ± 0.4	1-8.5
Cattle Egret	others	3.2	841	1.4 ± 0.1	0.4-3.45	8.0 ± 0.7	5-25
Squacco Heron	others	1.8	56	1.5	—	2.0	—
Black-crowned Night-Heron	Total	—	205	14.6 ± 2.7	0.1-300	8.8 ± 0.6	1-50
Little Egret	Total	—	503	2.2 ± 0.1	0.5-50	3.9 ± 0.2	0.5-15
Cattle Egret	Total	—	841	0.9 ± 0.1	0.1-28	3.1 ± 0.1	1-25
Squacco Heron	Total	—	56	3.5 ± 1.2	0.1-64	4.4 ± 0.4	1.5-22

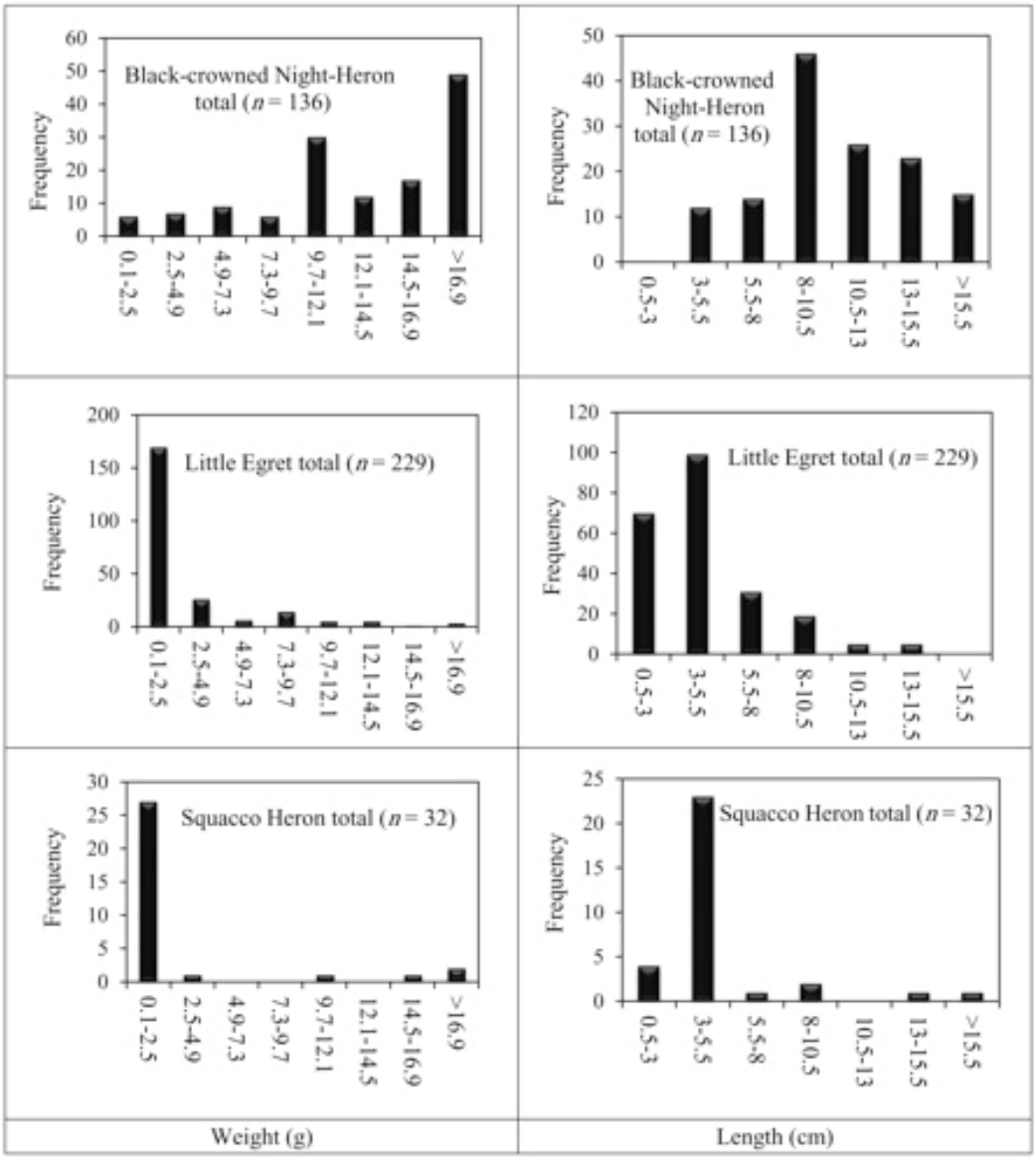

Figure 1. Frequency distributions by weight (g) in left column and length (cm) in right column of whole prey in regurgitates taken from Black-crowned Night-Herons, Little Egrets and Squacco Herons in the Anzali wetland in 2016.

mean weight was 4.3 g ± 2.2 g (Range = 0.1-64.0 g, $n = 32$) (Table 2). Of 32 fish regurgitates from Squacco Herons, 23 (71.8%) were between 3.0 and 5.5 g and 27 (84.3%) were between 0.1 and 2.5 cm in length (Fig. 1).

Interspecific Comparisons

There were significant differences between the weights ($\chi^2_3 = 318$, $P < 0.001$) and lengths ($\chi^2_3 = 225$, $P < 0.001$) of prey items among the four heron species. Weights of fish, amphibians and other items were significantly different ($\chi^2_2 = 198.4$, $P < 0.001$, $\chi^2_3 = 121.1$, $P < 0.001$ and $\chi^2_3 = 11.6$, $P < 0.01$, respectively), but insects did not show any significant difference ($\chi^2_3 = 7.6$, $P > 0.05$).

The fish items in Black-crowned Night-Heron regurgitates were significantly heavier and longer than in Squacco Heron and Little Egret regurgitates in all age classes (0-14 ($\chi^2_2 = 13.9$,

$P < 0.001$, $\chi^2_2 = 12.6$, $P < 0.001$, respectively), 15-28 ($\chi^2_2 = 22.4$, $P < 0.001$, $\chi^2_2 = 19.7$, $P < 0.001$,respectively) and > 28 days ($\chi^2_2 = 169.1$, $P < 0.001$, $\chi^2_2 = 161.4$, $P < 0.001$, respectively); Tables 3 and 4). Frequency distributions of weight (g) and length (cm) of Black-crowned Night-Heron, Little Egret and Squacco Heron chicks in different age categories are given in Figs. 2 and 3. These results indicate that chicks of the Black-crowned Night-Heron in all age categories received longer and heavier prey items compared with Little Egret and Squacco Heron chicks of the same age.

Approximately 52% of total prey items in three species, namely Black-crowned Night-Herons (66.3%), Little Egrets (45.5%) and Squacco Herons (57.1%), were fish. About 72% of total mass of regurgitates in Black-crowned Night-Herons (92.3%), Little Egrets (50.3%) and Squacco Herons (70.9%) were also fish. Among the chicks of these three ardeid species that fed on fish, the Little Egret had a more diverse diet and prey items than the other two species, and preyed mainly upon smaller prey (Table 2). Of 205 prey items of the Black-crowned Night-Heron, 58.5% were from the Cyprinidae, 10.2% from Ranidae, and 3.9% from Araneidae (Table 1). Black-crowned Night-Herons took larger fish and amphibians than those taken by the other species, and the size of prey items was smallest for the Little Egret (Table 2). In addition, Black-crowned Night-Herons fed on large prey such as reptiles and mammals, which were absent from the diets of the Little Egret and the Squacco Heron (Table 2).

Little Egret regurgitates contained 503 items from seven Orders and 24 families. Of these 503 prey items, 119 (23.6%) were from the Poeciliidae, 17.1% from the Cyprinidae and 11.7% from the Ranidae (*Rana ridibunda*). Twelve of 24 families were identified in Little Egrets, with 26.8% of total prey items and 32.3% of mass belonging to insects. Among the total 841 prey items of the Cattle Egret, 53.7% were from the Araneidae, 10.8% from the Tabanidae, and 7.1% from the Ricaniidae, with the remainder coming from 20 other prey families. Of 56 prey items of the Squacco Heron, 48.3% were from the Cyprinidae and 27.6% from the Ranidae, with the remainder coming from eight other prey families (Table 1). There was little dietary overlap using the Pianka Overlap Index, with the exception being between the Black-crowned Night-Herons and Squacco Herons (0.92) (Table 5).

DISCUSSION

A number of studies have suggested that diet analyses based on regurgitated items are potentially biased (Delord *et al.* 2004; Jakubas 2005; Ashoori *et al.* 2012; Ashoori and Rakhshbhar 2013). This study profiled the nestling diets of chicks of four heron species at Ghalam-Goodeh in the Anzali wetland. Our results showed that four ardied species had diverse diets both in terms of the prey items taken and the size classes. The most common prey items recorded across four species were fish, amphibians, insects and arachnids. Fish were especially important in the diets of the Back-crowned Night-Heron, Little Egret and Squacco Heron when compared with the Cattle Egret. Insects and arachnids (total of 94.4%) represented the largest number of prey items, and insects had the most weight in the diet

Table 3. Total weight (g) of fish items consumed by Black-crowned Night-Heron, Little Egret and Squacco Heron chicks in three age categories in the Anzali wetland in 2016. In each row, means followed by different letters are significantly different (Mann-Whitney *U*- test, $P < 0.05$).

	Total Weight (g)			
Age (days)	Black-crowned Night-Heron	Little Egret	Squacco Heron	*P*-value
0-7	9.1 ± 1.1^{a} ($n = 6$)	$0.4 \pm 0.07^{b,b}$ ($n = 9$)	$1.7 \pm 0.3^{a,c}$ ($n = 2$)	$P < 0.001$
8-15	11.6 ± 2.7^{a} ($n = 21$)	$4.4 \pm 1.7^{a,b}$ ($n = 8$)	$0.8 \pm 0.1^{a,c}$ ($n = 18$)	$P < 0.01$
> 16	22.7 ± 2.9^{a} ($n = 109$)	$2.6 \pm 0.3^{b,b}$ ($n = 212$)	$10.1 \pm 5.5^{c,b}$ ($n = 12$)	$P < 0.001$

Table 4. Total length (cm) of fish items consumed by Black-crowned Night-Heron, Little Egret and Squacco Heron chicks in three age categories in the Anzali wetland in 2016. In each row, means followed by different letters are significantly different (Mann-Whitney *U*- test, $P < 0.05$).

	Total Length (cm)			
Age (days)	Black-crowned Night-Heron	Little Egret	Squacco Heron	*P*-value
0-7	10.6 ± 1.0^{a} ($n = 6$)	$3.2 \pm 0.1^{b,b}$ ($n = 9$)	$3.5 \pm 0.5^{a,c}$ ($n = 2$)	$P < 0.001$
8-15	7.8 ± 0.8^{a} ($n = 21$)	$4.9 \pm 0.7^{a,b}$ ($n = 8$)	$3.7 \pm 0.2^{a,b}$ ($n = 18$)	$P < 0.01$
> 16	11.7 ± 0.5^{a} ($n = 109$)	$4.3 \pm 0.2^{b,b}$ ($n = 212$)	$6.4 \pm 1.8^{c,b}$ ($n = 12$)	$P < 0.001$

of chicks of the Cattle Egret. which reflects differences in foraging habitat.

Focusing on the diet components, it appears that the foraging habitat of the Black-crowned Night-Heron, Little Egret and Squacco Heron was around the Anzali wetland. The Black-crowned Night-Heron and Squacco Heron preyed more on Cyprinidae compared with the Little Egret. The Little Egret often was seen searching for food in open water areas of this wetland, while the other two species did not show similar behavior. The Little Egret ate more items, but they were smaller in length and weight. A greater variety of prey types, mainly small fish, have also been reported in the Little Egret diet from Axios Delta and Kerkini Lake (Kazantzidis and Goutner 2005). However, high prey variation in the Little Egret diet could be attributed to foraging in all available feeding habitats (Kazantzidis and Goutner 1996, 2005).

Although Black-crowned Night-Herons and Squacco Herons had many similarities in prey items, an obvious difference was found in the length and weight of fish items they ate. Black-crowned Night-Herons often feed next to water bodies or flowing water, while the Squacco Heron often was seen in wetland areas with a high volume of aquatic vegetation where it often is a suitable place for the growth of smaller fishes. These two herons could avoid competition by partitioning resources and using different feeding habitats.

The number of insects (especially Gryllotalpidae) was greatest in the Cattle Egret diet and constituted the largest mass in the Little Egret diet compared to the other two ardied species. This was also reported in Karfestan Ab-bandan, Iran, for the Little Egret (Ashoori 2010).

In Greece and France, the most important prey category was fish in the diets of the Little Egret nestlings (Kazantzidis *et al.* 1996; Kazantzidis and Goutner 2005), similar to the results in the present study, while in two other studies in Italy and Iran the contribution of fish in the diet was lower (Fasola *et al.* 1981; Ashoori 2010). Differences in prey items within diets primarily reflect differences in foraging habitats and distribution of prey (Kazantzidis and Goutner 2005).

Similarly, the diets of Black-crowned Night-Heron and Squacco Heron were dominated by fish species (especially Cyprinidae), similar to other studies in Spain (Perez *et al.* 1991), Italy (Fasola *et al.* 1981, 1993) and southern Europe (Fasola 1994) and in Kerkini Lake (Birtsas 2002). However, for Squacco Herons, amphibians were also found in appreciable proportions. The diet of the Squacco Heron in the Anzali wetland is contrary to results reported by Hancock and Kushlan (1984), Laszlo (1986) and Voisin (1991). In all of these studies, insects or amphibians predominated by number, although amphibians or fish had greater mass.

Sympatric herons and egrets use similar foraging habitats and prey types opportunistically (Fasola 1994; Kazantzidis and Goutner 2005; Post 2008), which could possibly cause competition particularly where diets overlap (Fasola and Cardarelli 2015). However, in the present study there was no significant overlap between the diet compositions of the Cattle Egret and three other heron species. Moreover, although not significant, there was more similarity between the Black-crowned Night-Heron and Little Egret, as well as the Little Egret and Squacco Heron. In contrast, Fasola and Cardarelli (2015) found minimum overlap between the Black-crowned Night-Heron

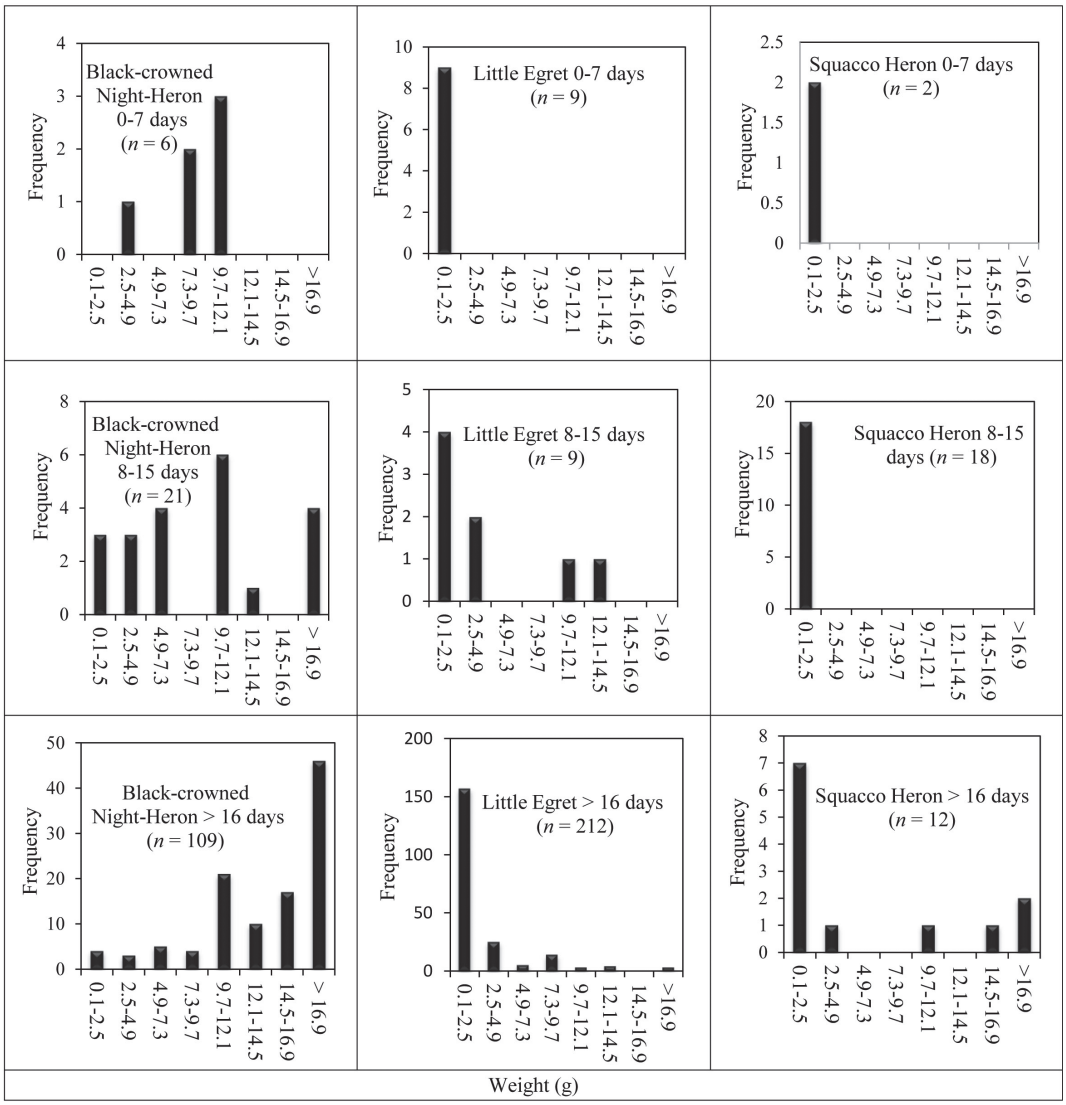

Figure 2. Frequency distributions by weight (g) of whole fish prey in regurgitates taken from Black-crowned Night-Heron, Little Egret, and Squacco Heron chicks in three age categories (0-7, 8-15 and > 16 days) in the Anzali wetland in 2016.

and Little Egret but high overlap between the Black-crowned Night-Heron and Squacco Heron in Italy. Such overlaps between heron species may suggest diet segregation on the basis of prey species (Tayefeh *et al.* 2014). Thus, this may explain how it occurred between the Cattle Egret, Black-crowned Night-Heron, Little Egret and Squacco Heron in our Iran study area and suggests that species may partition resources by using different prey types, feeding habitats and feeding techniques in mixed-species colonies (Smith 1997).

This study supports the findings of previous studies on dietary segregation in heronries (Fasola 1994; Kazantzidis and Goutner 2005). Our results offer support for the hypothesis of food resource partitioning limiting or reducing competition in areas where multiple species coexist. This is in keeping with conventional niche theory's segregation among sympatric populations or species in an *n*-dimensional niche hyper-volume to help ensure their co-existence (Hutchinson 1959; Holt 2009).

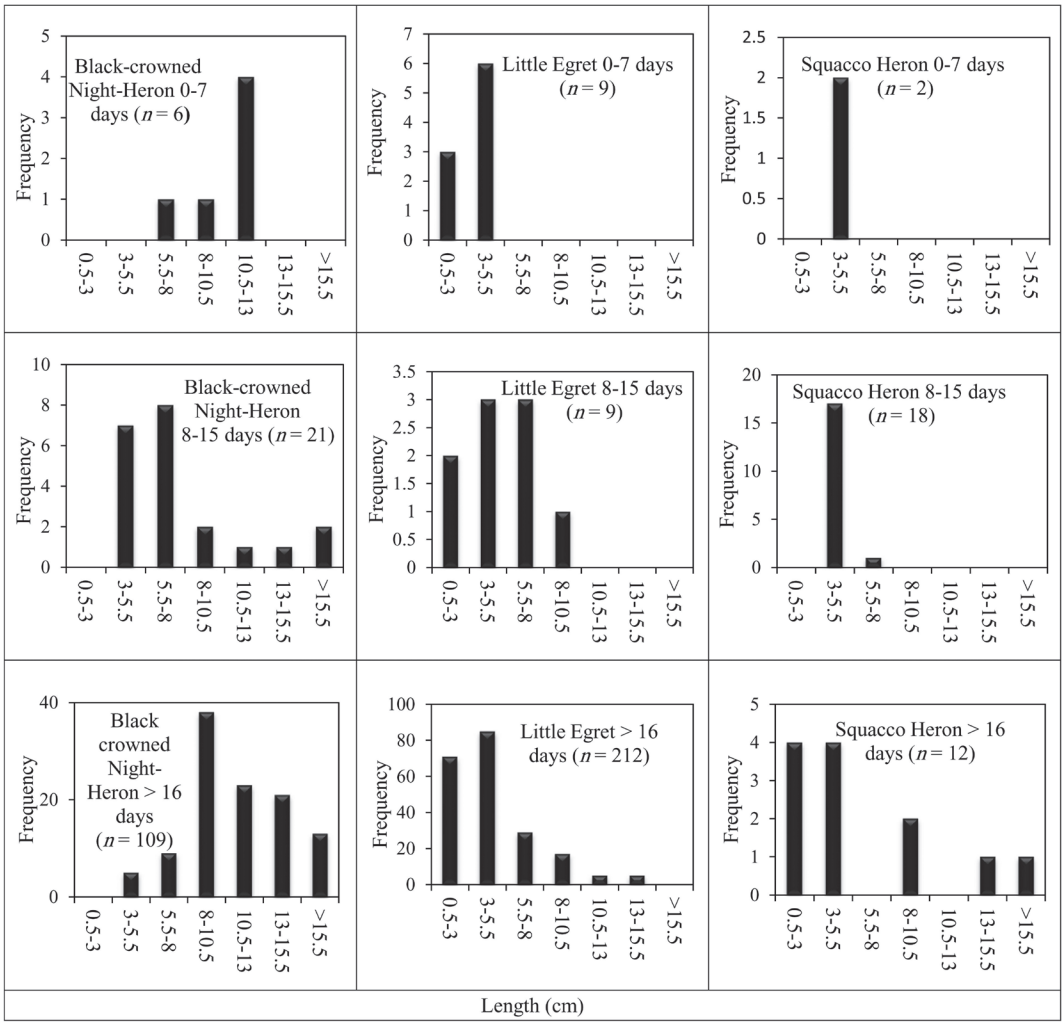

Figure 3. Frequency distribution by length (cm) of whole fish in regurgitates taken from Black-crowned Night-Heron, Little Egret and Squacco Heron chicks in three age categories (0-7, 8-15 and > 16 days) in the Anzali wetland in 2016.

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Table 5. Prey composition overlap between species using the Pianka Overlap Index (Pianka 1973). A number greater than 0.6 suggests a substantial degree of overlap in diets (highlighted in bold).

Species	Little Egret	Cattle Egret	Squacco Heron
Black-crowned Night-Heron	0.52	0.08	**0.92**
Little Egret	—	0.24	0.54
Cattle Egret	—	—	0.03

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