Long-Term Changes in Food Intake by Grey Herons (Ardea cinerea), Black-Crowned Night-Herons (Nycticorax nycticorax) and Little Egrets (Egretta garzetta) Foraging in Rice Fields in Italy

Authors: Cardarelli, Elisa, Fasola, Mauro, Martinoli, Adriano, and Pellitteri-Rosa, Daniele

Source: Waterbirds, 40(4) : 344-352

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.040.0406

Long-term Changes in Food Intake by Grey Herons (*Ardea cinerea*), Black-crowned Night-Herons (*Nycticorax nycticorax*) and Little Egrets (*Egretta garzetta*) Foraging in Rice Fields in Italy

ELISA CARDARELLI[1], MAURO FASOLA[1,*], ADRIANO MARTINOLI[2] AND DANIELE PELLITTERI-ROSA[1]

[1]Department of Earth and Environmental Science, University of Pavia, Via Ferrata 9, Pavia, Italy

[2]Department of Theoretical and Applied Sciences, University of Insubria, Via Dunant 3, Varese, Italy

[*]Corresponding author; E-mail: fasola@unipv.it

Abstract.—In northwestern Italy, traditional rice cultivation using permanent flooding has been replaced by cultivation that uses a reduced water depth and a shortened submersion period. Prey availability for the numerous herons and egrets using this intensive rice cultivation region changed as well, with a diminution of amphibians and an increase of crayfish (*Procambarus clarkii*) and oriental weatherfish (*Misgurnus anguillicaudatus*). The prey intake in 2014 was compared with data available for 1987 for the three most common species of waterbirds that forage in the paddies. Total biomass intake by Grey Herons (*Ardea cinerea*) feeding in the paddies decreased from 28 g dry mass/min in 1987 to 7 g in 2014, and by Black-crowned Night-Herons (*Nycticorax nycticorax*) from 8 g to 5 g, while the intake by Little Egrets (*Egretta garzetta*) remained similar (12 and 13 g in 1987 and 2014, respectively). The observed levels of prey intake allowed breeding Grey Herons to meet their energy needs by feeding exclusively in the rice paddies in 1987, but not in 2014. The other two study species could not meet their daily requirements for successful breeding by feeding in the paddies only, either in 1987 or 2014. Yet the three species bred successfully in the study area, and their reproductive output remained stable both in 1987 and 2014. Successful breeding was probable by the three species foraging in other habitats, such as rivers, small natural wetlands and irrigation canals, in the region. *Received 15 February 2017, accepted 30 May 2017.*

Key words.—*Ardea cinerea*, Black-crowned Night-Heron, *Egretta garzetta*, energy budget, food intake, Grey Heron, Little Egret, *Nycticorax nycticorax*, rice.

Waterbirds 40(4): 344-352, 2017

Rice paddies can act as a valuable substitute for natural wetlands, especially in the Mediterranean Basin where the seminatural wetlands have been reduced to only 10-20% of their historical area (Finlayson *et al.* 1992). This is particularly true for herons and egrets that obtain a large portion of their food resources from agro-ecosystems worldwide (Elphick *et al.* 2010). The intensive rice cultivation region in northwestern Italy hosts a large number of breeding Grey Herons (*Ardea cinerea*), Little Egrets (*Egretta garzetta*) and Black-crowned Night-Herons (*Nycticorax nycticorax*). During 1980-1990, these breeders obtained the bulk of their prey from the extensive network of irrigation canals and the rice paddies that were cultivated according to the traditional practice of permanent flooding from April to August with water depths from 10 to 30 cm (Fasola *et al.* 1996). This situation changed after 1995 when new and varied cultivation practices were adopted over large portions of the rice cultivation region to reduce costs for water purchase and management. Presently, most paddies are cultivated with dry seeding, and flooding has been shortened to May-August with water depths of only a few cm, with a prolonged period when the paddies remain muddy but without surface water (Ferrero 2007; Angelini *et al.* 2008; Romani 2008). A change also occurred after 1995 in the prey types available to the herons and egrets in northwestern Italy. During 1980-1990, amphibians were one of the staple prey species, but their numbers decreased sharply after 1995 and new allochthonous prey species appeared in the diet (Fasola and Cardarelli 2015).

Under the hypothesis that reduced flooding and changes in prey availability may have affected the suitability of the paddies for herons and egrets of northwestern Italy, the objectives of our study were to: 1) describe the prey intake of Grey Herons, Black-crowned Night-Herons and Little Egrets foraging in the rice paddies that were subjected to the changes in cultivation practices (a shorter May-August flooding period and shallower water depth); 2) assess the changes since

1987 in the suitability of the paddies of northwestern Italy as foraging habitat for the three study species; and 3) evaluate whether the three study species could meet their food demands during breeding by foraging exclusively in the rice paddies cultivated using current methods.

Methods

Study Area

We recorded foraging success at two study areas in 1987 and at five areas in 2014, scattered throughout the region of intensive rice cultivation in northwestern Italy (Table 1; Fig. 1). One of the areas was the same for both study periods, but the second 1987 area could not be resampled because of changes in land use in 2014. Therefore, during 2014 we were compelled to adopt new study areas within the relatively uniform region of rice cultivation, where the paddies cover large portions of the landscape. Each study area was within a flight distance of 5-10 km from one to three heronries.

In 2013-2014, we replicated the field techniques used from 1985 to 1988 to investigate the foraging ecology of the three study species, so as to allow a comparison between the two study periods. The original data for 1985 (Fasola 1986) and for 1987 and 1988 (M. Fasola, unpubl. data) were clumped and are hereafter referred to as "1987" data. The 1987 data were re-analyzed together with the new data for 2013-2014, which also were clumped and are hereafter referred to as "2014" data. The aim of assessing the long-term changes in the average foraging success justifies clumping the results for subsequent years into the two periods "1987" and "2014" spaced across three decades. The possible inter-annual differences were taken into account in the models.

Data Collection

Each study area was surveyed throughout the daylight hours, from 06:00 to 19:00 hr, once per week from 3 May to 22 June in 1985, 1987 and 1988, and from 7 May to 30 June in 2013 and 2014. This was when the proportion of nests with chicks was at its peak in the nearby heronries. We approached each adult bird that was actively foraging and in breeding plumage. Focal birds did not increase distance from the observer or appear to change behavior. A focal observation was performed on each bird by a single observer from a car at a distance from 30 to 80 m (the maximum distance of the birds in the paddies from our path). All observed focal birds were foraging in flooded or semi-flooded rice paddies that had been temporarily drained for cultural operations and maintained a partial water cover. In most cases, focal observations were conducted for 10 min (n = 532, 90.5% of observed birds) using spotting scopes (20-60x); in a few preliminary trials, sampling lasted more than 10 min (n = 56, 9.5% of observed birds). During each observation we recorded number, type, and size of captured prey. When visual identification of small prey type was dubious, their identity was confirmed at the end of each observation by net sampling at the spot where the focal bird had been feeding. Prey size was estimated in the field as a proportion of bird bill standard length, and was later calculated from the mean bill length values: 120.3 mm for Grey Heron (Cramp and Simmons 1977), and 72.4 mm for Black-crowned Night-Heron and 90.4 mm for Little Egret (measured on 12 and 16 individuals of both sexes, respectively, captured within our study area from 1989 to 2014). One of the observers collected records in each study year. All observers attended training sessions at the beginning of each year to ensure consistency in prey identification and size estimation.

For each focal bird observation, we calculated the intake of each prey type as biomass (g, dry mass/min). Biomass reflected the nutritional value more accurately than the number of items because the different prey types ranged in size over several orders of magnitude. We assigned a mass value to each captured prey item by using one of the three following estimates (details in Fasola and Cardarelli 2015). For small to medium size prey that had been identified to species or to the categories of Table 3, we assigned a mean mass based on a large sample of individuals of the same taxon; these prey samples were either obtained in the paddies after the focal observations or obtained whole from regurgitations by nestlings of the same heron and egret species within our study area and were then dried in an oven at 60 °C until a constant weight was obtained. For fish and other large prey, whose length had been recorded during the focal observations, we assigned the mass calculated from length-mass relationships, which were obtained from publications on the local fauna or calculated from sample specimens collected in the rice

Table 1. Study areas within the region of intensive rice cultivation in northwestern Italy.

Municipality	Study Year(s)	Coordinates of the Area Center		Total Surface Area of Rice Paddies (ha)
1 Zerbolò	1985, 2014	45° 12′ 38.4″ N	9° 01′ 36.1″ E	636
2 Galliavola	1987-1988	45° 04′ 44.4″ N	8° 49′ 22.8″ E	681
3 Mosezzo	2013	45° 26′ 32.8″ N	8° 30′ 28.2″ E	939
4 Ronsecco	2014	45° 14′ 52.8″ N	8° 14′ 24.0″ E	321
5 Morsella	2014	45° 16′ 15.6″ N	8° 49′ 22.8″ E	134
6 Vespolate	2014	45° 19′ 26.4″ N	8° 37′ 04.8″ E	634

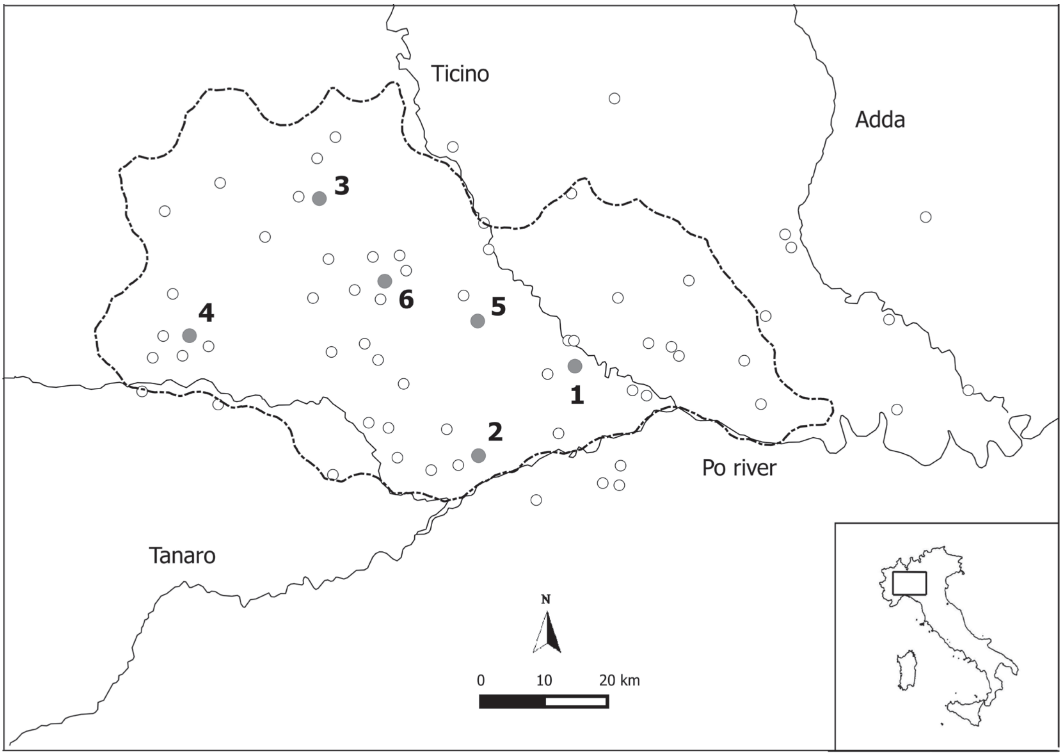

Figure 1. Study areas (gray circles, numbers as in Table 1) sampled for foraging success of Grey Herons, Black-crowned Night-Herons and Little Egrets in northwestern Italy. Dotted line: region of intensive rice cultivation; open circles: heronries; black lines: major rivers.

paddies during our study. The remaining unidentified small items were assigned a combined total mean dry mass based on all of the small items identified for the same heron species.

Data Analysis

We divided the foraging herons and egrets into two categories based on capture success: "successful" individuals that captured > 0 prey and "non successful" individuals that did not capture any prey during the 10-min focal observation. Differences in the percentage of successful and non-successful individuals between 1987 and 2014 were tested by Chi-square with Yates correction, or by Fisher's exact test when the number of observed animals was small (Fisher 1922; Yates 1934; Crawley 2007).

The difference in the number of captured prey items between the two study periods was compared for each prey category separately, using Generalized Linear Mixed Models (GLMMs) with a Poisson distribution and a log link function. The Poisson distribution is typically used for count data, and the log link function ensures positive fitted values. When necessary, we corrected for overdispersion of the data using a negative binomial distribution, that is again used for integers, non-negative data, when the variance is larger than the mean (Zuur *et al.* 2009). The study period was fitted as a fixed categorical factor (two levels: 1987 vs. 2014), while the site and the year of sampling were fitted as random factors to incorporate the dependency among observations carried out in the same site and in subsequent years. Log of the duration of the focal observations in minutes was used as an offset to account for the different length of each observation (Zuur *et al.* 2013). We compared the parsimony of the models with and without the year of sampling using the Akaike information criterion (AIC), and we removed the factor when the model was not improved (Burnham and Anderson 2002). For the infrequent prey (number of records < 15), and particularly for those that were not recorded in one of the two study periods, it was not possible to run the models due to the small number of records. The difference in the total biomass intake per minute from rice paddies between 1987 and 2014 was tested by Linear Mixed Effects (LME) models with the same structure of GLMMs described earlier. The biomass intake data were normalized by square-root transformation. All statistical analyses were performed using the statistical software R (R Development Core Team 2016), and the supplementary packages "car" (Fox and Weisberg 2011), "nlme" (Pinheiro *et al.* 2016) and "lme4" (Bates *et al.* 2015).

Energy Budget Estimates

Energy consumption and food demands of free-living birds can be predicted from body mass (Carey 1996;

Blem 1999). We calculated the Basal Metabolic Rate (BMR) for our three study species using the equation for non-passerines: BMR (in kcal/bird/day) = 0.522 * M (body mass in g) ^ 0.735 (Kendeigh *et al.* 1977). For M, we used the values of 1,433 g for Grey Heron (Cramp and Simmons 1977), 580 g for Black-crowned Night-Heron and 505 g for Little Egret. The Daily Energy Expenditure (DEE) is the sum of BMR plus the energy needed for physiological processes, muscular work, and tissue production; for DEE, we used the estimate of 3.6 * BMR, a value recorded in various species of breeding birds in the wild and over extended periods (King 1974; Blem 1999; Hodum and Weathers 2003). In addition to its own DEE, a breeding adult also needs to meet further demands from its nestlings. Therefore, we estimated the peak demands of a nestling from the equation for Peak Daily Metabolized Energy (PDME), which scales with body mass at fledging: PDME (in kj) = 5.01 M (in g) ^ 0.782 (Weathers 1992), using observed M values for Black-crowned Night-Heron nestlings at fledging in our study area (Prigioni *et al.* 1985). We obtained the number of nestlings from data on breeding success recorded at several heronries within our study area (Fasola 1998; E. Cardarelli, unpubl. data); the values for each study period, calculated as the mean of a sample of 19-53 nests for each species and year, were: 2.3 chicks/nest (1987 and 2014) for Grey Herons; 2.5 chicks/nest (1987 and 2014) for Black-crowned Night-Herons; and 3.5 (1987) and 3.3 chicks/nest (2014) for Little Egrets. The energetic value of each prey category was measured by bomb calorimetry of samples collected within our study areas (Table 2). A metabolized energy coefficient equal to 82.5% of the energetic value was adopted so as to account for digestive and assimilation efficiency (Causey 1999).

Finally, we calculated the amount of prey that a breeding adult Grey Heron, Black-crowned Night-Heron and Little Egret should collect to meet the peak daily energy expenditure for itself and its brood during nestling growth, using the above estimates of energy need, the mean number of chicks/nest in 1987 and in 2014, and the mean energetic content of prey taking into account the different proportion of prey types captured in 1987 and in 2014, as well as assuming a balanced biparental care (Fasola 1984; Hafner *et al.* 2002).

RESULTS

In 1987, we studied 142 focal individuals foraging in flooded paddies, recording 1,235 prey captures and identifying 85% of the prey. In 2014, we studied 446 focal birds and recorded 3,832 prey captures, of which 44% could be identified. The proximity of large heronries with several hundred breeding pairs made it unlikely that we would have repeatedly observed the same individuals, although some double counting could have occurred. We used only adult birds in breeding plumage for our sample, but we might have included a few non-breeders.

Prey Type

The prey types in 2014 differed considerably from those in 1987 (Table 3). The primary difference was that new prey species appeared in 2014. The mole cricket (*Gryllotalpa* sp.) and two allochthonous species, the Louisiana crayfish (*Procambarus clarkii*) and the oriental weatherfish (*Misgurnus anguillicaudatus*), invaded our study area after 1990. In addition, worms and small crustaceans belonging to the genus *Triops* were more frequent in 2014, while frogs and tadpoles were less frequent. The larvae of large aquatic insects were not recorded in 2014, although smaller larvae could have been present among the non-identified small prey (Table 3).

Food Intake

The proportion of successful individuals that had captured at least one prey during

Table 2. Energy content of the main prey categories. The values are the mean of three samples, each made by one item for larger prey, or by a composite of several individuals for worms, arthropods and tadpoles.

Prey Category	Dry Prey (kJ/g)
Worms (Lumbricidae)	20.40
Louisiana crayfish (*Procambarus clarkii*)	15.31
Other aquatic arthropods	19.27
Mole cricket (*Gryllotalpa* sp.)	20.89
Other terrestrial arthropods	21.68
Oriental weatherfish (*Misgurnus anguillicaudatus*)	20.50
Other fish	20.16
Tadpoles of green frog (*Pelophylax* kl. *esculentus*)	11.74
Adult green frogs (*Pelophylax* kl. *esculentus*)	22.69
Snakes (*Natrix* sp.)	23.10

Table 3. Prey captured in rice paddies by the three study species during the two study periods. Values are percentage of occurrence of each taxon. Insects and amphibians are metamorphosed, if not otherwise specified.

	Grey Heron		Black-crowned Night-Heron		Little Egret	
Prey Category	1987	2014	1987	2014	1987	2014
Worm (Oligochaeta)	0.00	9.93	28.44	39.30	6.63	10.01
Crustacean (Notostraca, *Triops cancriformis*)	17.14	32.35	3.06	0.96	2.51	10.59
Crustacean (Louisiana crayfish, *Procambarus clarkii*)	0.00	0.00	0.00	0.32	0.00	0.06
Insect (mole cricket, *Gryllotalpa* sp.)	0.00	1.47	0.00	3.19	0.00	0.03
Insect (undetermined)	0.29	0.00	0.00	0.00	0.00	0.00
Insect larvae (undetermined)	27.71	0.00	0.00	0.00	0.18	0.00
Fish (oriental weatherfish, *Misgurnus anguillicaudatus*)	0.00	11.03	0.00	2.56	0.00	2.37
Fish (undetermined)	0.29	0.00	0.00	0.32	0.36	0.34
Adult green frog (*Pelophylax* kl. *esculentus*)	7.71	4.04	11.01	10.54	8.06	0.52
Tadpole of green frog (*Pelophylax* kl. *esculentus*)	36.29	16.18	47.40	16.29	61.29	14.78
Newt (Salamandridae, *Triturus carnifex*)	0.00	0.00	0.31	0.00	0.36	0.00
Snake (Colubridae, *Natrix* sp.)	0.29	0.00	0.00	0.00	0.00	0.00
Undetermined	10.29	25.00	9.79	26.52	20.61	61.29
Total number of items	350	272	327	313	558	3,247
Total number of focal individuals	33	91	62	171	47	184

focal observation decreased from 1987 to 2014 for Grey Herons (82% in 1987 vs. 55% in 2014) and for Black-crowned Night-Herons (71% in 1987 vs. 43% in 2014). These values differed significantly for both species (χ^2 = 6.33, df = 1, P = 0.007 and χ^2 = 13.45, df = 1, P < 0.001, respectively). However, for Little Egrets the proportion of successful individuals was the same in both periods, 92% (χ^2 = 0.001, df = 1, P = 0.98).

The capture rate by the three studied species (Table 4; Fig. 2) differed significantly between 1987 and 2014 for the main staple prey, even if at the edge of significance in some cases. Frogs were captured at slower rates in 2014 by the three species, particularly by Grey Herons and Little Egrets. The same tendency is also evident for tadpoles. On the contrary, the capture rate of fish was higher in 2014, especially for Little Egrets. The total biomass intake was much lower in 2014 than in the previous period for both Grey Herons and for Black-crowned Night-Herons, while it was similar for Little Egrets (Table 5).

Energy Budget

The total amount of prey that a single individual needed to meet the collective Peak

Table 4. Estimates (± SE) of intercept and covariate coefficients for the GLMMs comparing prey captured by the three studied species in 1987 and 2014. A separate model was run for each prey type (df always equal to 1); intercept estimate represents prey captures in 1987 while covariate estimate represents prey captures in 2014.

Species	Prey Types	Intercept (± SE)	Covariate (± SE)	χ^2	P
Grey Heron	Frog	-3.16 (0.9)	-2.31 (1.2)	3.57	0.059
	Tadpole	-1.06 (1.1)	-2.92 (1.6)	3.35	0.067
	Fish	-6.34 (1.3)	2.33 (1.3)	3.05	0.081
Black-crowned Night-Heron	Frog	-2.95 (0.6)	-1.17 (0.7)	2.72	0.099
	Tadpole	-1.59 (1.8)	-4.32 (2.2)	3.71	0.054
	Worm	-1.95 (0.7)	-0.54 (0.8)	0.41	0.52
Little Egret	Frog	-2.51 (0.6)	-2.28 (0.8)	8.88	0.003
	Tadpole	-0.11 (0.7)	-1.45 (0.8)	3.46	0.063
	Fish	-5.5 (0.9)	2.23 (1.0)	5.18	0.023
	Worm	-3.06 (1.2)	-0.10 (1.4)	0.01	0.943

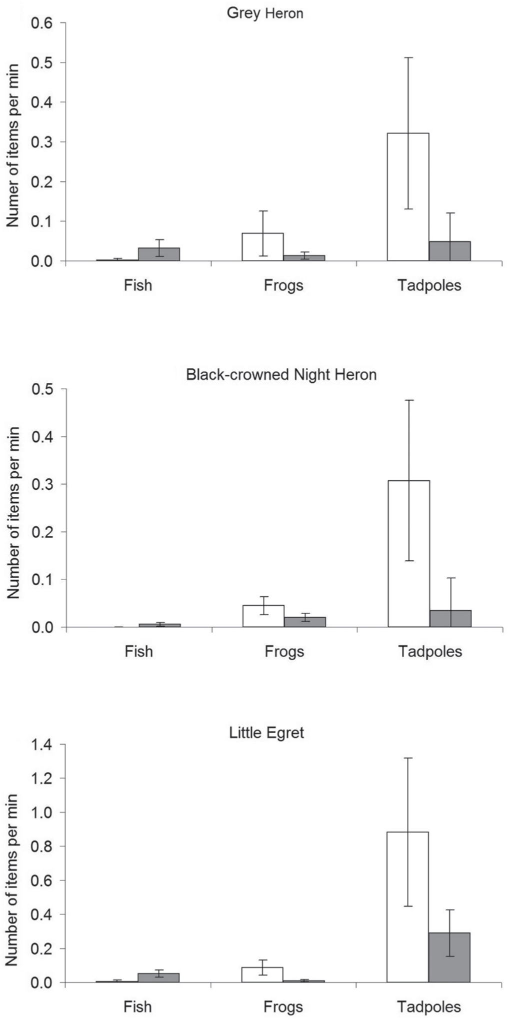

Figure 2. Capture rate (mean number of captured items/min ± 95% CI) in the two study periods (white bars for 1987, gray bars for 2014) for the prey types whose capture rate differed at $P < 0.1$.

Daily Energy Expenditure for reproduction was estimated for Grey Herons at 207 g (1987) and 216 g (2014) dry mass/day, for Black-crowned Night-Herons at 104 g (1987 and 2014) dry mass/day, and for Little Egrets at 115 g (1987) and 112 g (2014) dry mass/day. From these food requirements and from the observed values of prey intake (Table 5), we calculated the time needed by a bird foraging only in the flooded paddies to satisfy its peak daily requirement for itself plus its brood. One breeding Grey Heron would have satisfied its requirement by foraging for 12 hr per day in 1987, while the diminished prey intake was largely insufficient to meet requirements in 2014 when 51 hr per day would have been necessary. The intake by Black-crowned Night-Herons was already insufficient to meet the daily requirements in 1987 when one bird would have to forage for a non-sustainable 22 hr per day, and it was even more insufficient in 2014 when 35 hr would have been required. Only the relatively higher prey intake by Little Egrets could have allowed individuals to meet the daily requirements of a breeder by foraging for 16 hr per day in 1987 and for 14 hr per day in 2014.

DISCUSSION

The prey intake of Grey Herons and Black-crowned Night-Herons foraging in the rice paddies declined sharply from the 1987 study period to the 2014 study period. With such low levels of prey intake, successful breeding by Grey Herons foraging in paddies only was not possible in 2014. For Black-crowned Night-Herons, the foraging conditions had already been deteriorating since 1980, when they could meet their daily requirements for breeding by foraging in the paddies of the same study area for 8 hr/day due to a higher prey intake (22 g dry mass/day during daytime) (Fasola 1984). Breeding Black-crowned Night-Herons could not have met their requirements by feeding in paddies only, neither in 1987 nor in 2014, even taking into account that the species can forage both during day and night on the same prey types (Fasola 1984). Only the Little Egrets had a prey intake that might have allowed successful breeding, both in 1987 and in 2014, although the required effort (foraging for 16 hr and 14 hr per day, respectively) could hardly have been sustainable for this species that forages only during daytime, which in our study area lasts from 14 to 15 hr in May and June during the peak nestling period. A similar result was found by Sizemore and Main (2012) in the Everglades, Florida, USA, where Little Blue Herons (*E. caerulea*) foraging in rice paddies could meet their ener-

Table 5. Mean biomass intake (in g dry mass/min ± SE) from rice paddies for the three studied species during 1987 and 2014, and significance of the differences (df always equal to 1).

	1987	2014	F	*P*
Grey Heron	0.28 (0.14)	0.07 (0.01)	13.8	0.014
Black-crowned Night-Heron	0.08 (0.01)	0.05 (0.01)	1.88	0.229
Little Egret	0.12 (0.01)	0.13 (0.01)	0.19	0.683

gy requirements while Great Egrets (*Ardea alba*) could not.

Despite declined prey intake, the reproductive output of our study species in 1987 and in 2014 remained the same (Fasola 1998; E. Cardarelli, unpubl. data). We believe this is related to a higher food intake from habitats other than the paddies, such as rivers, small natural wetlands and the extended network of irrigation canals that carry the water from the rivers to each paddy. We observed large numbers of herons and egrets feeding in these habitats, but it was not possible to record their prey intake. The importance of foraging habitats other than the paddies is supported by a comparison of the prey captured in the paddies with the nestling diet recorded in a parallel study (Fasola and Cardarelli 2015) on the same species, in the same study area, and during a similar period (2013). Some staple prey were much more frequent in the nestling diet (Fasola and Cardarelli 2015) than in the intake from the paddies. Such differences were particularly large for the Louisiana crayfish (Black-crowned Night-Heron: 12.7% in chick diets vs. 0.03% from foraging in the paddies only; Little Egret: 18.7% in chick diets vs. 0.1% from foraging in the paddies only), the oriental weatherfish (Black-crowned Night-Heron: 14.8% in chick diets vs. 2.6% from foraging in paddies only; Little Egret: 10.0% in chick diets vs. 2.4% from foraging in paddies only), the mole criket (Black-crowned Night-Heron: 14.3% in chick diets vs. 3.2% from foraging in paddies only; Little Egret: 7.3% in chick diets vs. 0.03% from foraging in paddies only), and fish other than the weatherfish (Black-crowned Night-Heron: 5.8% in chick diets vs. 0.3% from foraging in paddies only; Little Egret: 5.2% in chick diets vs. 0.3% from foraging in paddies only). Moreover, Fasola and Cardarelli (2015) found that the availability of metamorphosed amphibians and tadpoles in the paddies was lower in 2013 than in the preceding three decades. These differences imply that in 2014 Louisiana crayfish, oriental weatherfish, mole cricket, and some fish were obtained from habitats other than the rice paddies. A higher prey intake in these other habitats might have allowed the successful breeding that was recorded in our two study periods.

The suitability of rice paddies in northwestern Italy as foraging habitat for breeding herons and egrets has sharply decreased during the past four decades due to changes in cultivation practices and concomitant changes in prey types. However, the reproductive output of the three study species remained similar, probably because the breeders are able to compensate the lower prey intake from paddies by foraging in other habitats (irrigation canals that are part of the agro-ecosystem, the few seminatural wetlands, and the rivers). The paddies continue to be used by many foraging herons and egrets despite the diminishing prey intake especially for Grey Herons and Black-crowned Night-Herons.

The number of colonies and the total number of nests of herons and egrets in northwestern Italy had markedly increased during the period from 1975-1995 thanks to climatic factors and a diminished human-induced mortality (Fasola *et al.* 2010). After 2000, the trend was reversed, with a decrease in the number of nests of all the species except for the Cattle Egret (*Bubulcus ibis*), a partially terrestrial feeder (Fasola 2017). This decreasing trend might have been affected by the changes in prey type (Fasola and Cardarelli 2015) and by the diminished prey intake that was documented by the present study for the paddies that are now cultivated throughout northwestern Italy with shortened submersion and shallow water. Another change in the cultivation practices that is decreasing the suitability of the paddies for waterbirds comes from the recent spread of turned irrigation without submersion throughout the cultivation cycle from April to September. Ranghetti *et al.* (2016) estimated that the paddies in northwestern Italy remained completely dry during May and June in increasing proportions, from very small surfaces in 2000 up to 33% of the total surface area of paddies in 2014.

Acknowledgments

We are indebted to Damiano Preatoni and Francesco Bisi for the calorimetric measurements, to the anonymous referees for their suggestions, and to Jeff Dolphin (University of Nevada, USA) for the English revision. Bird capture was authorized by Regione Lombardia (decree 1598, 27 February 2014). This project was partially supported by the Italian Ministry of Education, University and Research (PRIN 2010-2011, 20108 TZKHC).

Literature Cited

Angelini, R., A. Ferrero and I. Ponti (Eds.). 2008. Il riso. Bayer CropScience, Bologna, Italy. (In Italian).

Bates, D., M. Maechler, B. Bolker and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1-48.

Blem, C. R. 1999. Energy balance. Pages 327-341 *in* Avian Physiology (W. G. Causey, Ed.). Academic Press, San Diego, California.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York, New York.

Carey, C. 1996. Avian energetics and nutritional ecology. Springer, New York, New York.

Causey, W. G. 1999. Avian physiology. Academic Press, San Diego, California.

Cramp, S. and K. E. L. Simmons (Eds.). 1977. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, vol. I: ostrich to ducks. Oxford University Press, Oxford, U.K.

Crawley, M. J. 2007. The R book. John Wiley & Sons Ltd., Chichester, U.K.

Elphick, C. S., K. C. Parsons, M. Fasola and L. Mugica (Eds.). 2010. Ecology and conservation of birds in rice fields: a global review. Waterbirds 33 (Special Publication 1): 1-246.

Fasola, M. 1984. Activity rhythm and feeding success of nesting Night-Herons *Nycticorax nycticorax*. Ardea 72: 217-222.

Fasola, M. 1986. Resource use of foraging herons in agricultural and nonagricultural habitats in Italy. Colonial Waterbirds 9: 139-148.

Fasola, M. 1998. Optimal clutch size in herons: observational and experimental approaches. Ethology Ecology & Evolution 10: 33-46.

Fasola, M. 2017. Il monitoraggio delle garzaie nel 2016 - 45° anno. Unpublished report, Università di Pavia, Pavia, Italy. http://ecoeto.unipv.it/component/jdownloads/viewdownload/37/160?Itemid=0, accessed 23 May 2017. (In Italian).

Fasola, M. and E. Cardarelli. 2015. Long-term changes in the food resources of a guild of breeding Ardeinae (Aves) in Italy. Italian Journal Zoology 82: 238-250.

Fasola, M., L. Canova and N. Saino. 1996. Rice fields support a large portion of herons breeding in the Mediterranean region. Colonial Waterbirds 19 (Special Publication 1): 129-134.

Fasola, M., D. Rubolini, E. Merli, E. Boncompagni and U. Bressan. 2010. Long-term trends of heron and egret populations in Italy, and the effects of climate, human-induced mortality, and habitat on population dynamics. Population Ecology 52: 59-72.

Ferrero, A. 2007. Rice scenario in the European Union. Cahiers Agricultures 16: 272-277.

Finlayson, C. M., G. E. Hollis and T. J. Davis (Eds.). 1992. Managing Mediterranean wetlands and their birds. International Waterfowl and Wetlands Research Bureau Special Publication No. 20, Slimbridge, U.K.

Fisher, R. A. 1922. On the Interpretation of χ^2 from contingency tables, and the calculation of P. Journal of the Royal Statistical Society 85: 87-94.

Fox, J. and S. Weisberg. 2011. An R companion to applied regression, 2nd ed. Sage Publications, Thousand Oaks, California. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion, accessed 21 April 2017.

Hafner, H., M. Fasola, C. Voisin and Y. Kaiser. 2002. *Egretta garzetta* Little Egret. Journal of Birds of the Western Palearctic 1: 1-19.

Hodum, P. J. and W. W. Weathers. 2003. Energetics of nestling growth and parental effort in Antarctic fularine petrels. Journal of Experimental Biology 206: 2125-2133.

Kendeigh, S. C., V. R. Dol'nik and V. M. Gavrilov. 1977. Avian energetic. Pages 127-204 *in* Granivorous Birds in Ecosystems (J. Pinkowski and S. C. Kendeigh, Eds.). Cambridge University Press, Cambridge, U.K.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pages 4-85 *in* Avian Energetics (R. A. Paynter, Ed.). Nuttall Ornithological Club Publication 15, Cambridge, Massachusetts.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and R Core Team. 2016. nlme: linear and nonlinear mixed effects models v. 3.1-128. R Foundation for Statistical Computing, Vienna, Austria. http://CRAN.R-project.org/package=nlme, accessed 21 April 2017.

Prigioni C., P. Galeotti and M. Fasola. 1985. Accrescimento dei pulli e riuscita della riproduzione della Nitticora *Nycticorax nycticorax*. Avocetta 9: 127-133. (In Italian).

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/, accessed 21 April 2017.

Ranghetti, L., L. Busetto, A. Crema, M. Fasola, E. Cardarelli and M. Boschetti. 2016. Testing estimation of water surface in Italian rice district from MODIS satellite data. International Journal of Applied Earth Observation and Geoinformation 52: 284-295.

Romani, M. 2008. Tecnica colturale. Pages 298-323 *in* Il riso (R. Angelini, A. Ferrero and I. Ponti, Eds.). Bayer CropScience, Bologna, Italy. (In Italian).

Sizemore, G. C. and M. B. Main. 2012. Quality of flooded rice and fallow fields as foraging habitat for Little Blue Herons and Great Egrets in the Everglades agricultural area, USA. Waterbirds 35: 381-393.

Weathers, W. W. 1992. Scaling nestling energy requirements. Ibis 134: 142-153.

Yates, F. 1934. Contingency tables involving small numbers and the χ^2 test. Supplement to the Journal of the Royal Statistical Society 1: 217-235.

Zuur, A., J. M. Hilbe and E. N. Ieno. 2013. A beginner's guide to GLM and GLMM with R: a frequentist and Bayesian perspective for ecologists. Highland Statistics Ltd., Newburgh, U.K.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev and G. M. Smith. 2009. Mixed effects models and extensions in ecology. Springer, New York, New York.