

The diet of nestlings of three Ardeidae species (Aves, Ciconiiformes) in the Axios Delta, Greece

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ABSTRACT. The diets of the little egret (*Egretta garzetta*), the night heron (*Nycticorax nycticorax*) and the squacco heron (*Ardeola ralloides*) were studied by analyzing nestling regurgitations collected during five breeding seasons (1988-1990 and 1994-1995) at a heronry in the Axios Delta (Northern Greece). In total, 267 regurgitations from little egrets, 247 from night herons and 19 from squacco herons (only in 1995) were collected and analyzed. Each prey item was identified to the lowest possible taxon. The dry mass of each prey taxon was also estimated from oven-dried prey specimens collected in the field.

At least 58 different prey taxa were identified among 5,108 items found in little egret regurgitations, at least 45 taxa among 2,373 items regurgitated by night herons and 12 taxa among 277 items from squacco herons regurgitations. Differences were detected between the three ardeid species in the proportion of each prey category. Little egret nestlings were mainly fed fish (39.6% by number) and insects (32.0%), but amphibians and fish were the most important groups by biomass (44.9% and 32.9% respectively). The proportions of prey categories varied significantly between years ($\chi^2_{12} = 922.91$, $p < 0.001$). The night heron nestlings were mainly fed insects and the crustacean *Triops cancriformis*, although the dry mass of the latter contributed little to the consumed biomass (4.0% compared to the 37.9% of insects). Small mammals and reptiles were included in the diet of the young night herons, while the fish they ate were much bigger than those consumed by little egret nestlings. The proportions of the night herons' main prey categories varied significantly between years ($\chi^2_{24} = 598.67$, $p < 0.001$). Squacco heron chicks were fed mainly insects (50.9%) and amphibians (31.8%), the latter being more important by biomass (73.6%). In a cluster analysis, diet of young little egrets and night herons showed greater similarity from 1988 to 1990 than between 1994 and 1995, suggesting temporal changes in prey use. Study years tended to group separately for each species, but those of the little egret were more scattered in the cluster than the night heron's, thus reflecting greater prey use variability. The diet of the squacco heron was similar to that of the little egret when prey type frequencies were considered, but closer to the night heron's by dry mass. The dry mass differed significantly between the species ($\chi^2 = 87.39$, $p < 0.001$, Kruskal-Wallis test). This dietary segregation may be a mechanism that reduces competition among these ardeid species, especially when prey is limited.

KEY WORDS : Ardeidae, diet, Axios, little egret, night heron, squacco heron

INTRODUCTION

The little egret (*Egretta garzetta* Linnaeus, 1766), the night heron (*Nycticorax nycticorax* Linnaeus, 1758) and the squacco heron (*Ardeola ralloides* Scopoli, 1769) breed in a multi-species colony in the Axios Delta. These ardeid species share certain foraging habitats, such as freshwater marshes and rice fields, but exploit them in different proportions (FASOLA, 1994). The little egret exploits all aquatic habitats in the Axios Delta, including salt marshes and the seashore, whereas the other two herons forage only in freshwater habitats. Thus, although the three sympatric species may be considered generalists, they seem to be separated ecologically by their selection of different prey type or size.

The diet of the three study species is poorly known in Greece. Studies concerning the diet of the little egret are available from Kerkini Lake (TSACHALIDIS, 1990) and the Axios Delta (FASOLA 1994 ; KAZANTZIDIS et al., 1996 ; KAZANTZIDIS, 1998). The diet of the night heron has been studied at the Kerkini Lake (BIRTSAS, 2002), while the squacco heron data presented here are the first published for

Greece. The diet of the three ardeid species has been studied in more detail in other Mediterranean countries : France (VALVERDE, 1956 ; HAFNER, 1977 ; VOISIN, 1991), Italy (MOLTONI, 1936 ; FASOLA et al., 1981, FASOLA et al., 1993 ; FASOLA, 1994), Spain (GONZALES-MARTIN & GONZALES-SOLIS, 1990 ; PEREZ et. al., 1991 ; MARTINEZ et. al., 1992) and Israel (ASHKENAZI and YOM-TOV, 1996). Although, the diet of various herons has often been studied in the western Palearctic multiyear studies comparing the diet of sympatric species are generally scarce. The objectives of this study were to describe the diets of these three ardeid species, and to compare them between species and years. For the squacco heron we have data from 1995 only, and are therefore unable to present a comparison between years.

MATERIAL AND METHODS

The study was carried out in the Axios Delta, northern Greece (40° 30' N, 22° 53' E), part of a large wetland complex situated in the western part of Thermaikos Gulf (N. Aegean Sea). It extends over 68.7 km² and comprises

estuarine and deltaic areas, with a variety of natural and man-made habitats such as salt and fresh water marshes, ricefields, vegetated islets, river banks, tamarisk shrubland, and sandy shores (ATHANASSIOU, unpublished data). This wetland complex is of international importance according to the Ramsar convention, and a Special Protected Area.

The heron colony where the regurgitations were collected is located in a riverine forest of Tamarisks (*Tamarix* spp.), Willows (*Salix* spp.) and Alders (*Alnus glutinosa*), on an island near the mouth of the River Axios. This colony is the second biggest in Greece in terms of both number of breeding pairs and number of species (KAZANTZIDIS, 1998). Other breeding species were great cormorants (*Phalacrocorax carbo* Linnaeus, 1758), pygmy cormorants (*Phalacrocorax pygmaeus* Pallas, 1773), spoonbills (*Platalea leucorodia* Linnaeus, 1758) and glossy ibises (*Plegadis falcinellus* Linnaeus, 1766). The total breeding population of the colony ranged, in recent years from 1,100 to 2,000 pairs (KAZANTZIDIS, 1998).

Heron diet was studied by analyzing nestling regurgitations collected during the breeding seasons of 1988-1990 and 1994-1995 (squacco heron data were collected only in 1995). Regurgitations were collected throughout each nestling period, on a weekly basis, from April until early July. After collection, the regurgitations were refrigerated until analysis. In order to estimate the quantitative contribution of each prey type, the dry mass of each prey taxon was measured. Samples from each prey type were collected during the nestling period from the main feeding habitats (ricefields, irrigation canals, salt- and freshwater marshes). Dry mass was measured by weighing each prey taxon dried in an electric oven for 48 hours at approximately 70°C. Intact items found in the regurgitations were also used for the estimation of their dry mass.

In order to compare the frequencies of items from the different prey categories between years, we used Chi-square tests. We used Mann-Whitney U-tests and Kruskal-Wallis χ^2 tests to compare median prey dry mass between the study species. In order to identify the diet similarities or differences between the three study species and the years of the study, a cluster analysis was applied to the proportions of main prey categories in each study species X year combination.

RESULTS

We collected 533 regurgitations in total (267 from little egrets, 247 from night herons and 19 from squacco herons). In these we identified 7,758 prey items with a total

dry mass of 3,207 g belonging to 74 different taxa (Appendix 1).

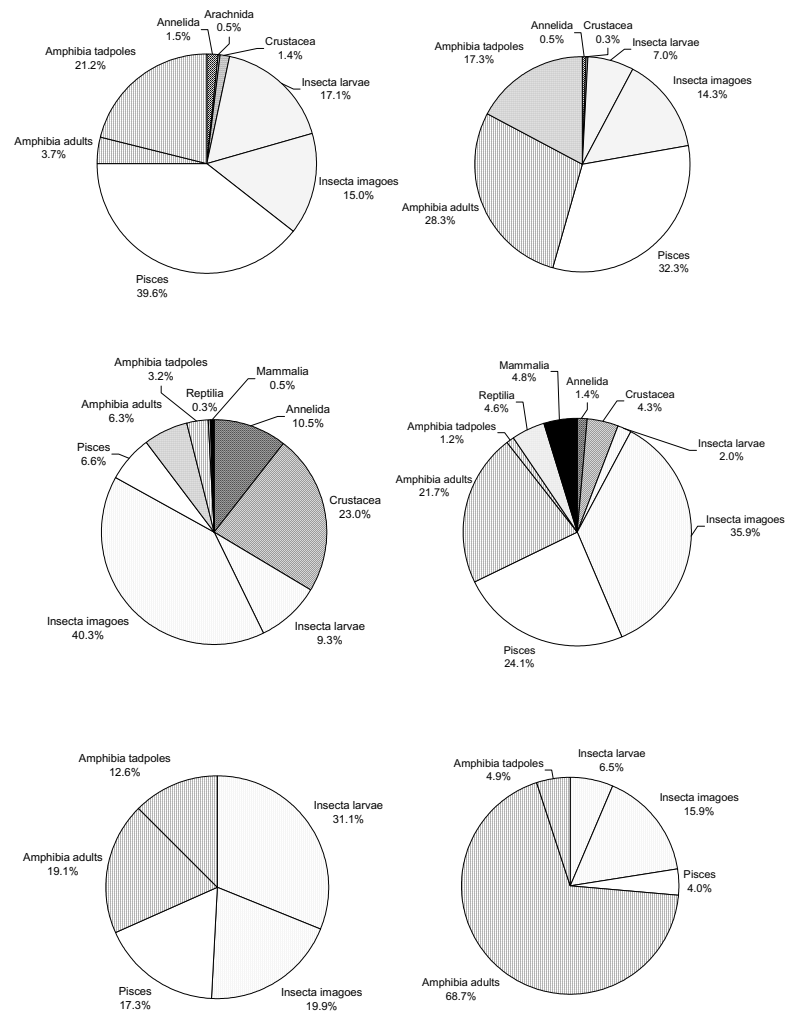


Fig. 1. – The diets of nestlings of the little egret (top), night heron (middle) and squacco heron (bottom) by number (left) and by dry mass (right) of the main prey categories.

Little egret

At least 58 different taxa were identified among 5,108 prey items (1,499 g dry mass). By number, fish were the most important prey category (39.6%), followed by insects (32.1%) and amphibians (24.9%) (Fig.1). From a total of 22 fish species identified, *Aphanius fasciatus*, *Gambusia affinis* and *Gasterosteus aculeatus* represented 85.5% of all items. Of at least 27 species of insects, the majority were larvae of Odonata, Dytiscidae and Hydrophilidae (94.3% of all insect larvae). Among imagoes, *Gryllotalpa gryllotalpa* and *Zygoptera* spp. (Odonata) prevailed, making up 72.2% of all items. Tadpoles predominated among amphibians (85.0%), while the adults were mainly *Rana ridibunda* and *Hyla arborea*. annelids (*Lumbricus terrestris*), arachnids (mainly *Argyroneta aquatica*) and crustaceans (Gammaridae and the

phyllopod *Triops cancriformis*) contributed less to the diet and were not present in all study years (Figs 1-2).

By dry mass, amphibians and fish were the most important food resources (45.6% and 32.3%, respectively, of the total dry mass) (Fig. 1). Each of the other prey categories contributed less than 1% (Fig. 1). The average dry mass of all prey items was $0.29g \pm 0.72$ (Table 1).

TABLE 1

The average dry mass (\pm SD) of the main prey categories consumed by the three ardeid species

Prey type	Little Egret	Night Heron	Squacco Heron	Kruskal-Wallis χ^2 1
Insects	0.20 \pm 0.26	0.50 \pm 0.31	0.27 \pm 0.29	379.4
Fish	0.24 \pm 0.96	2.37 \pm 5.43	0.14 \pm 0.13	221.5
Amphibians	0.53 \pm 0.69	1.56 \pm 0.93	1.43 \pm 0.97	337.2
Others	0.03 \pm 0.04	0.11 \pm 0.01	0	-17.38 ²
Total	0.29 \pm 0.72	0.65 \pm 1.7	0.62 \pm 0.81	87.39

1. $p < 0.0001$ in all cases.

2. Mann-Whitney U-test was applied. Annelids, crustaceans and arachnids only are included.

Diet composition differed between years ($\chi^2_{12} = 922.91$, $p < 0.001$). Within the main prey categories, the differences were also significant (fish: $\chi^2_4 = 598.72$, $p < 0.001$; insects: $\chi^2_4 = 369.65$, $p < 0.001$; amphibians: $\chi^2_4 = 159.6$, $p < 0.001$) (Fig. 2).

Night heron

At least 45 different taxa were found among 2,373 prey items (1,537 g dry mass). Insects (at least 22 taxa) were by far the most numerous prey (49.6%), followed by crustaceans (exclusively *T. cancriformis*) (23.1%), amphibians (9.5%) and fish (6.6%). Annelids (*Lumbricidae*) also contributed in relatively high proportion (10.5% by number), although they appeared only in three out of five study years (Figs 1-2). Reptiles (*Natrix natrix* and *Emys orbicularis*) and mammals (*Arvicola terrestris*, *Microtus arvalis*, *Rattus* spp.) were also found in low proportions (Figs 1-2). The majority of insects were imagoes (81.3% of all insect items), predominantly *G. gryllotalpa* (77.8% of all imagoes and 31.3% of all prey items). Amphibians were mainly adult *R. ridibunda* (66.7%). Of 13 fish species found in the regurgitations, *Leuciscus cephalus*, *Carassius auratus* and *Lepomis gibbosus* were the most numerous (58.3% of all fish items). By dry mass, insects were the most important category (37.9%), followed by fish (24.1%) and adult amphibians (21.7%) (Fig. 1). The average dry mass of all prey items was $0.65g \pm 1.7$ (Table 1).

Diet composition differed between years, both considering all prey types ($\chi^2_{24} = 598.67$, $p < 0.001$), and within each of the main prey categories (fish: $\chi^2_4 = 41.45$, $p < 0.05$; insects: $\chi^2_4 = 184.36$, $p < 0.001$; amphibians: $\chi^2_4 = 102.48$, $p < 0.001$). The number of mammals and reptiles did not differ between years ($\chi^2_4 = 8.07$, $p = 0.089$ and $\chi^2_4 = 2.56$, $p = 0.633$, respectively) (Fig. 2).

Squacco heron

The 277 prey items found (171 g dry mass) belonged to at least 12 different taxa. By number insects (eight species

and 50.9% of all prey items) were the most important prey category, followed by amphibians (31.8%) and fish (17.3%) (Fig. 1). The majority of insects (61.0%) were larvae (mainly Odonata, Dytiscidae and Hydrophilidae), while imagoes were mainly *G. gryllotalpa* (65.5% of all imagoes). Amphibians were mainly adults of *R. ridibunda* (60.2% of all amphibians). Of the three fish species found, *G. affinis* was the most numerous (81.3%).

By dry mass, *R. ridibunda* was the most important prey taxon (68.7% of the total dry mass), followed by *G. gryllotalpa* (15.9%), whereas fish represented only 4.0% of the total (Fig. 1). The average dry mass of all prey items was $0.62g \pm 0.81$ (Table 1).

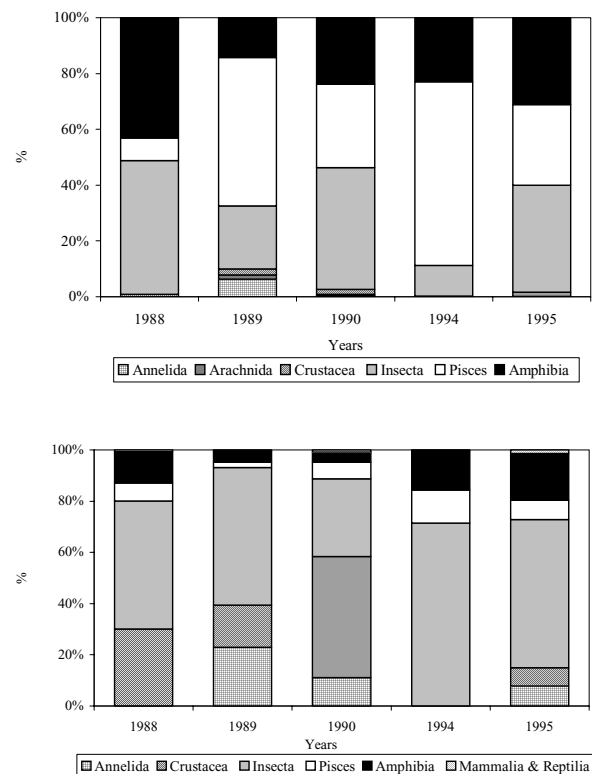


Fig. 2. – The yearly composition of the diet (by number of the main prey categories) of the little egrets (top) and night herons (bottom).

Interspecific comparison

The little egret had a more diverse diet than the other two species, and preyed mainly upon small-sized prey. Both fish and amphibians (mainly tadpoles) eaten by little egrets were small-sized (average dry masses of $0.24g \pm 0.96$, and $0.21g \pm 0.69$ respectively).

The median prey dry mass differed significantly between the three ardeid species as a result of the smaller average dry mass of prey of the little egret (Table 1).

The night herons took insects, fish and amphibians of larger size than those taken by the other two species (Table 1). In addition, night herons fed on large prey such as reptiles and mammals, which were absent from the diet of the little egret and the squacco heron (Fig. 1, Appendix 1). Crustaceans (*T. cancriformis*) were also absent from the diet of these two species while they were common in the night heron's diet. This difference may be due to the

absence of *T. cancriformis* from the foraging areas during the nestling period of the little egret and the squacco heron, but its availability to night herons, which start breeding at least two weeks earlier than the other two species (FASOLA et al., 1981, KAZANTZIDIS et al., 1997).

Of 74 different taxa identified in the nestlings' regurgitations, 37 were common to the three ardeid species while only four (namely *R. ridibunda*, Dytiscidae and Hydrophilidae larvae, and *G. gryllotalpa*) participated in proportions of more than 10% of all prey items in the diets of all three ardeid species.

The diets of the squacco heron and the little egret shared 11 species in common (Fig. 3, Appendix 1), while a higher resemblance was found between the diets of the little egret and the night heron (31 common species or taxa). Only nine species or taxa were common to the squacco and the night herons' diets.

Inter-year comparison

Differences between years were detected, and the diets of both the little egret and the night heron showed greater similarity from 1988 to 1990 than between 1994 and 1995, suggesting temporal changes in prey use (Figs 2-3). Study years tended to group separately for each species, but those of the little egret were more scattered in the cluster, indicating a greater prey use variability (Fig. 3).

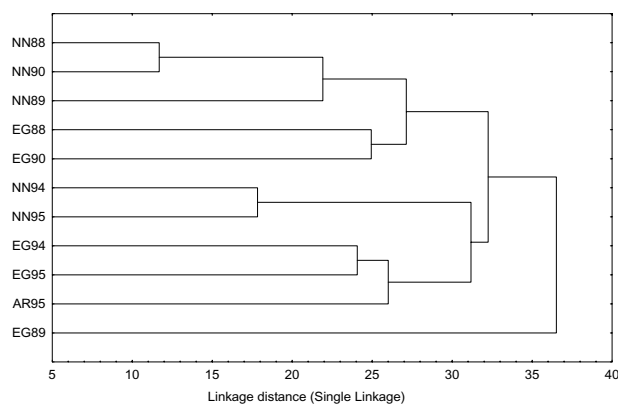


Fig. 3. – Comparison of the diet (by prey categories) between the three ardeid species and study years (EG : little egret, NN : night heron, AR : squacco heron).

DISCUSSION

The three ardeid species considered in this study had distinctive diets. Little egrets took a wide variety of prey types and fed mainly on small-sized fish, insects and tadpoles. Similar findings have also been reported from Kerkini Lake (TSACHALIDIS, 1990) although the size of fish there was larger (up to 9.3 cm) and *T. cancriformis* contributed to the diet in a higher proportion (up to 8.1%). In the Camargue, S. France, freshwater fish also predominated in the diet of little egrets' nestlings (HAFNER, 1977 ; KAZANTZIDIS et al., 1996). In Italy the contribution of fish to the diet was smaller, but still significant (28.07%) (FASOLA et al., 1981). Generally, although differences have been detected even among different colonies of the

same area, fish seems to be the most important prey for the little egret (VOISIN, 1991).

Night herons fed heavily on insects (especially *G. gryllotalpa*), which were the most important prey category by both number and dry mass. *T. cancriformis* and annelids were present in only some years of the study. Fish and amphibians were not common (both less than 10% of all prey items). These findings differ from those of all other studies of this species' diet conducted in Greece and in other Mediterranean countries. BIRTSAS (2002) reported that in Kerkini Lake the nestlings' diet consisted mainly of fish (86.5%) and amphibians (12.1%), while insects represented only 1.5% of all prey items. Similarly, fish was the night heron's major food type (93.7%) in Extremadura, Spain, (PEREZ et al., 1991), in Israel (ASHKENAZI & YOM-TOV, 1996) and in Serbia (LASZLO 1986). Furthermore, FASOLA et al. (1981, 1993) and FASOLA (1994) reported that in various Italian colonies, fish (Cyprinidae) or amphibians dominated the diet, while insects were found in very low proportions. In the Camargue, night herons feed mostly on fish and coleopteran larvae (VALVERDE, 1956 ; HAFNER, 1977). The great geographical variability in the night heron's diet probably reflects differences in prey availability in each breeding area and a great flexibility in prey use by this species.

The diet of the squacco heron at the Axios Delta is similar to that reported by MOLTONI (1936), CRAMP & SIMMONS (1977), HAFNER (1977), HANCOCK & KUSHLAN (1984), LASZLO (1986) and VOISIN (1991). In all of the above studies, insects or amphibians predominated by number, although amphibians or fish had greater dry mass. Differences between colonies were found in Italy (FASOLA et al., 1993 ; FASOLA 1994), where fish (Cyprinidae) was the most frequent prey type in two out of three heronries, whereas insects participated in small proportions in all three colonies.

Dietary differences between the years of our study also indicate that these ardeid species are opportunistic foragers, changing their diet from one year to the next according to prey abundance and availability. For example, crustaceans, which were taken by both the little egret and the night heron, were completely absent in 1994 from both species' diet, suggesting a decrease of crustacean population in that year. Where studies of more than one year are available, they report temporal differences. In 1970, little egrets in the Camargue preyed mainly on insects, while in 1971 fish and crustaceans were more frequent (more than 50%) (HAFNER 1977). In the same study, no differences were detected in the proportions of prey types in the night and squacco herons.

The differences in prey taken by the three study species reflect mainly differences in their foraging habitats and distribution of prey. Little egrets were foraging in all available feeding habitats (KAZANTZIDIS & GOUTNER, 1996), which may account for the high prey variation reported in this study. Night and squacco herons avoid open habitats and forage mainly in fresh water marshes and occasionally in ricefields, thus limiting the range of prey types they can capture. The differences in prey dry mass also indicate a dietary segregation between the ardeid species.

In conclusion, there is a dietary segregation between the three ardeid species with regard to both relative frequencies and dry mass of prey types. There is a partitioning of food resources by foraging habitats and/or choice of prey. This resource partitioning may be a mechanism that reduces competition among the species, especially when prey is limited.

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APPENDIX 1

The prey species (number of items) identified in the nestling regurgitations of the three ardeid species

Species	<i>Egretta garzetta</i>	<i>Nycticorax nycticorax</i>	<i>Ardeola ralloides</i>
Prey type			
INVERTEBRATES			
ANNELIDA			
Oligochaeta			
Lumbricidae	-	68	-
<i>Lumbricus terrestris</i>	79	149	-
<i>Allolopophora</i> spp.	-	3	-
<i>Eisenia foetida</i>	-	30	-
ARTHROPODA			
Chelicerata			
<i>Argyroneta aquatica</i>	9	-	-
<i>Pholcus phalangoides</i>	1	-	-
Unidentified Arachnida	14	-	-
Crustacea			
Phillopoda			
<i>Triops cancriformis</i>	36	547	-
Amphipoda			
Gammaridae	32	-	-
Talitridae	2	-	-
Decapoda			
Palaemonidae	3	-	-
Insecta			
Odonata			
Larvae	328	31	35
Imagoes			
Zygoptera	276	22	5
<i>Platycnemis</i> spp.	2	-	-
Anisoptera	9	18	-
Aeshnidae	46	-	7
Libellulidae	30	-	-
Unidentified Odonata			
Orthoptera			
Acrididae	3	8	2
Tetrigidae	1	-	-
Tettigoniidae	3	-	-
Gryllotalpidae			
<i>Gryllotalpa gryllotalpa</i>	276	744	36
Unidentified Orthoptera	-	1	-
Dictyoptera - Mantodea	1	-	-
Hemiptera - Heteroptera			
Naucoridae	2	1	-
<i>Llyocoris cimicoides</i>	8	-	-
Notonectidae			
<i>Notonecta glauca</i>	5	-	-
Gerridae			
<i>Gerris lacustris</i>	9	-	-
<i>Aquarius najas</i>	1	-	-
Scutelleridae			
<i>Eurygaster maura</i>	1	-	-
Lygaeidae	-	2	-
Unidentified Hemiptera	7	5	2
Diptera			
Cyclorrhapha			
Tachinidae	1	-	-
Calliphoridae	1	-	-
Syrphidae	18	2	-
Brachycera			
Stratiomyidae imagoes	7	1	3
Stratiomyidae larvae	25	26	-
Tabanidae larvae	-	-	1
Unidentified Diptera	5	2	-
Hymenoptera	3	3	-
Apocrita	2	1	-
Formicidae	-	1	-
Coleoptera			
Carabidae	-	15	-
<i>Amara aenea</i>	-	2	-
Scarabaeidae	1	5	-
Elateridae imagoes	1	2	-
Elateridae larvae	-	2	-

Species	<i>Egretta garzetta</i>	<i>Nycticorax nycticorax</i>	<i>Ardeola ralloides</i>
Coccinellidae	-	16	-
<i>Coccinella 7-punctata</i>	2	14	-
<i>Propylea 14-punctata</i>	-	1	-
Chrysomelidae	1	2	-
<i>Leptinotarsa decemlineata</i>	-	1	-
Dytiscidae imagoes	22	37	-
Dytiscidae larvae	275	82	31
<i>Lybius</i> spp.	-	2	-
Hydrophilidae imagoes	2	15	-
<i>Laccobius</i> spp.	2	-	-
<i>Laccobius sinuatus</i>	-	1	-
<i>Hydrophilus piceus</i>	-	1	-
Hydrophilidae larvae	218	75	-
<i>Hydrophilus piceus</i>	25	2	19
Heteroceridae			
<i>Heterocerus flexuosus</i>	-	1	-
Unidentified Coleoptera	16	32	-
VERTEBRATES			
Pisces			
Cyprinidae	2	2	-
<i>Leuciscus cephalus</i>	5	17	-
<i>Cyprinus carpio</i>	4	-	-
<i>Pseudorasbora parva</i>	1	2	-
<i>Rutilus rutilus</i>	8	8	1
<i>Carassius auratus</i>	7	15	-
<i>Phoxinus phoxinus</i>	4	1	-
<i>Rhodeus sericeus</i>	18	-	1
<i>Alburnus alburnus</i>	2	2	-
Cobitidae			
<i>Cobitis</i> spp.	3	-	-
<i>Cobitis taenia</i>	2	-	-
Gasterosteidae			
<i>Gasterosteus aculeatus</i>	150	-	-
Poeciliidae			
<i>Gambusia affinis</i>	567	-	39
Centrarchidae			
<i>Lepomis gibbosus</i>	2	12	-
Gobiidae			
<i>Gobius</i> spp.	21	-	-
<i>Knipowitschia caucasica</i>	2	-	-
<i>Pomatoschistus</i> spp.	3	1	-
Clupeidae			
<i>Sardina pilchardus</i>	1	-	-
Atherinidae			
<i>Atherina</i> spp.	68	6	-
<i>Atherina boyeri</i>	24	1	-
Cyprinodontidae			
<i>Aphanius fasciatus</i>	1013	6	-
Mugilidae			
<i>Liza saliens</i>	2	-	-
Blenniidae			
<i>Blennius pavo</i>	8	-	-
Pleuronectidae			
<i>Platichthys flesus</i>	1	-	-
Soleidae			
<i>Solea solea</i>	4	-	-
Exocoetidae	-	2	-
Unidentified fish	95	81	7
Amphibia			
<i>Rana ridibunda</i>	158	95	52
<i>Hyla arborea</i>	9	1	-
<i>Rana</i> spp. adults	24	54	1
<i>Rana</i> spp. tadpoles	1084	75	35
Reptilia			
<i>Natrix natrix</i>	-	6	-
<i>Emys orbicularis</i>	-	1	-
Mammalia			
<i>Arvicola terrestris</i>	-	1	-
<i>Microtus arvalis</i>	-	2	-
<i>Rattus</i> spp.	-	2	-
Unidentified mammals	-	7	-
TOTAL	5108	2373	277