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Nestling diet of three sympatric egret species: rice fields support breeding egret populations in Korea

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Abstract The diets of the Intermediate Egret *Egretta intermedia*, Little Egret *E. garzetta*, and Cattle Egret *Bubulcus ibis* were examined by analyzing nestling regurgitations collected during the breeding season in 2005 at a colony in Asan, South Korea. Intermediate Egret nestlings mainly fed on insects (86.7% of total prey items), but fish were the most important group by biomass (64.3% of total biomass). Little Egret nestlings fed mainly on insects and fishes (43.4% and 33.2% of total items, respectively), and fish contributed 64.2% to the total biomass consumed. Cattle Egret chicks were mainly fed invertebrate prey (96.5% of total items), such as insects and spiders, which comprised just 64.3% of the total biomass of their diet. Loaches and aquatic insect larvae (mainly Odonata and Coleoptera) comprised a large proportion of the nestling diet of the three egret species. This suggests that all species forage primarily in rice fields, which represented the most extensive habitat surrounding the breeding colony.

Key words *Bubulcus ibis*, *Egretta garzetta*, *Egretta intermedia*, nestling diet, prey habits, rice fields

Many herons and egrets nest together in breeding colonies. Food availability or access to suitable feeding habitats is critical to establishment of a successful breeding colony (Hafner 1997, 2000). A breeding colony can be maintained if adequate surface area of the necessary feeding habitats is provided and if prey populations are large enough to meet the birds' requirements (Hafner 2000).

Rice fields can play an important role for many water bird populations, including herons and egrets, as their feeding habitat. As natural shallow wetlands gradually decrease and are degraded, the role of rice fields becomes more significant especially during the breeding period of egrets, which coincides with the rice-growing season (Fasola & Ruiz 1996; Lane & Fujioka 1998; Nam et al. 2015).

In Korea, herons and egrets commonly breed in multi-species colonies that include Grey Heron *Ardea cinerea*, Great Egret *A. modesta*, Little Egret *Egretta garzetta*, Intermediate Egret *E. intermedia*, Cattle Egret *Bubulcus ibis*, and Black-crowned Night Heron *Nycticorax nycticorax* (Park 2002). Rice fields are the dominant feeding habitat surrounding the majority of heronries and many egretries (Choi et al. 2007; Lee et al. 2012). Although most heron species use rice fields as feeding habitat, some species are more dependent than others on rice fields. As Intermediate and Cattle egrets in Korea are reported to forage regularly in flooded fields throughout their breeding period, and sometimes on levees between rice fields when paddies become densely vegetated, they clearly have a strong preference for rice fields as feeding habitat (Choi et al. 2007). Little Egrets forage in rivers and and at reservoirs as well as rice fields in Korea, but feed more frequently in rice fields than in other habitats during the breeding period (Choi et al. 2007; Lee et al. 2012).

European heron populations have shown an increasing trend in area with rice fields (Tourenq et al. 2000; Fasola et al. 2010), and the distinct increases in the Korean egret populations may have been driven by a similar availability of rice fields. The habitat ranges of both Cattle and Little egrets have expanded

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considerably in Korea since their first breeding was reported in the 1960s; now these species are common nationwide (Park 2002). The nesting population of Intermediate Egrets in Korea is considered to be stable, having increased less than the other species, and its colonies are concentrated mainly in the middle-western part of Korea in the areas of large expanses of rice fields (Park 2002; Choi 2008). It is thus possible that the size and distribution of flooded rice fields has a significant effect on breeding populations of herons and egrets. However, because the relationships between population dynamics and feeding habitats are complex and vary temporally among regions and species, study of the food habits is important to manage egret populations and preserve their habitat.

In this study, we examined the composition of the nestling diet of three rice-field dependant egret species: Intermediate, Cattle, and Little. Our objective was to compare the relative importance of food items in the diet of each species' nestlings. We discuss the effects of the availability of feeding habitat, especially rice fields, on their nestling diet, and differences between the nestling diets of the three species in relation to their prey preferences and microhabitat preferences within rice fields.

MATERIALS AND METHODS

We collected regurgitations of nestlings of the three ardeid species at a breeding colony (36°52′21″N, 127°01′54″E) in Asan City, Chungcheongnam-do, South Korea, during the brood-rearing period (May–June) in 2005. The colony included approximately 600 nests of six tree-nesting ardeids: Grey Heron (16.1%), Great Egret (4.8%), Intermediate Egret (11.3%), Little Egret (19.4%), Cattle Egret (21.0%), and Black-crowned Night Heron (27.4%). The colony was surrounded primarily by agricultural landscapes such as rice fields, irrigation channels, and reservoirs, with rice fields occupying the largest area. Egret species shared certain foraging habitats, such as freshwater marshes and rice fields, but the proportional use of these habitats differed among species. Three small egret species (Intermediate, Little, and Cattle) used flooded rice fields more frequently than other freshwater habitats (reservoir and stream) during their nestling period (Choi et al. 2007). However, Grey Heron, Great Egret, and Black-crowned Night Heron mainly used reservoirs, rivers, and irrigation channels for acquiring food, although they sometimes foraged at rice fields during the breeding season (Choi et al. 2007).

When visiting the colony for banding and for breeding biology studies, we also collected regurgitated food boluses from 2-3 weeks old young egrets (one sample from each nest). A total of 69 regurgitated food boluses from three species were collected, from 24 Intermediate Egret nests, 27 Little Egret nests, and 18 Cattle Egret nests. All prey remains were preserved in 70% ethanol solution at the time of collection and refrigerated until analysis. Prey remains varied from completely undigested to partially digested, but all items could be identified at least to class level. We identified and classified each prey item into the following broad taxonomic groups: fish, amphibians, crustaceans, spiders, insects, annelids, and bivalves. Fish were subsequently identified to genus or species; most invertebrates were identified only to order. To estimate the quantitative contribution of each prey type, we measured the dry mass of each taxon. Fish and frogs were measured to the nearest 1 mm (standard length for fish and snout-vent length for frogs). We estimated body length of partially digested prey items in comparison to completely undigested samples of the same species, separated undigested items from the boluses to the extent possible, and dried the undigested items in an electric oven for 48 hr at approximately 70°C. The dried taxa were weighed to the nearest 0.01 g. For small invertebrates (e.g., spiders and insects) with low variation in size and mass, we estimated total dry mass per bolus by multiplying the averaged values by the total abundance in each bolus. For fish and frogs, we compared dry mass with length-mass regressions to estimate biomass of the prey items in relation to body size.

We determined the habitat type of each prey item based on surveys of fauna in rice paddy ecosystems (Han et al. 2010, 2011) and additional field collections in the study area (Yu-Seong Choi and Hyung-Kyu Nam unpublished data), using three habitat classifications: (1) flooded rice paddies; (2) grasslands (terrestrial habitats), including earthen banks of rice fields; and (3) other freshwater habitats, including reservoirs and streams next to the colony.

Nestlings were captured under a permit from the local government (Asan City, Chungnam Province) and all procedures in the colony complied with general regulations concerning animal welfare and were approved by an ethics committee.

1) Dietary analysis

We expressed the composition of the diet of each

egret species as: (1) the numerical number and percentage of each prey item in comparison to all prey numbers; (2) the percent occurrence of each prey item (i.e., regurgitated boluses containing a given prey item as a percentage of all analyzed boluses); and (3) biomass, estimated as dry mass. Shannon's Index was used to estimate the trophic diversity of each species' diet (Magurran 1988; Krebs 1989) as follows:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i$$

where s is the number of different types of prey and p_i is the proportion of the i^{th} category of prey items. We estimated evenness as the ratio of H':H_{max}, where $H_{max}=\ln(s)$ or the maximum possible diversity for a given number of prey items.

We estimated dietary overlap among the three ardeid species using Schoener's Similarity Index (SSI) (Linton et al. 1981):

$$SSI = 1 - \left(1/2 \sum_{i=1}^{s} |p_{ij} - p_{ik}| \right)$$

where s is the number of prey types and p_{ij} and p_{ik} are the relative proportions of the i^{th} prey type in the diet of species j and k.

2) Statistical analysis

The trophic diversity among the three species was compared using non-parametric Kruskal–Wallis tests followed by multiple pairwise comparisons with Dunn's test. We performed all statistical analyses in STATISTICA (StatSoft 2004). All tests were two-tailed with a significance level of $P<0.05$.

RESULTS

1) Intermediate Egret

Eighteen types of prey were identified among 1,268 prey items in 24 boluses regurgitated by Intermediate Egret chicks. Insects were the most numerically frequent prey, followed by fish and spiders (Table 1). Coleoptera larvae (water beetles) and nymphs of Odonata (dragonflies and damselflies, 19.2%) comprised large proportions of the insect prey (Fig. 1).

Table 1. Comparison of prey composition of three egret species, determined by prey number (% N), presence/absence in boluses (% S), and biomass (% B) at a breeding colony in Asan, Korea in 2005.

Taxon (Class)	Intermediate Egret			Little Egret			Cattle Egret		
	% N	% S	% B	% N	% S	% B	% N	% S	% B
Pisces	9.8	83.3	64.3	33.2	96.3	64.2	2.4	33.3	7.7
Amphibia	0.9	16.7	3.0	10.9	51.9	12.9	0.9	61.1	27.1
Bivalvia	—	—	—	3.2	18.5	0.2	—	—	—
Malacostraca	0.1	4.2	0.1	6.3	22.2	4.7	0.1	5.6	0.1
Arachnida	2.3	45.8	0.9	0.5	11.1	0.2	19.6	100.0	16.4
Insecta	86.7	100.0	30.6	43.4	81.5	16.8	76.9	100.0	47.9
Others	0.2	12.5	1.1	2.5	7.4	1.0	0.1	11.1	0.8
Total	1,268	24	89.4	1,237	27	90.7	2,377	18	78.0

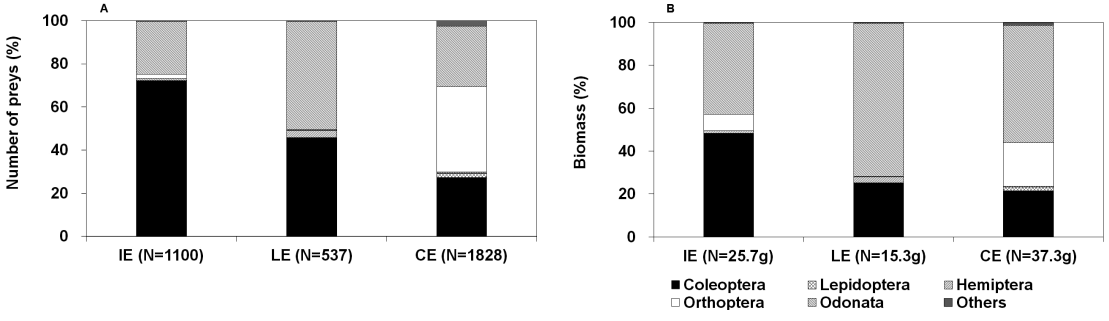

Fig. 1. The proportion of primary insect taxa (order) in diets of the Intermediate Egret (IE), Little Egret (LE), and Cattle Egret (CE), by number (a) and by dry mass (b).

By dry mass, fish (mostly loaches) were the most important prey provided to Intermediate Egret chicks, and insects (mostly Coleoptera larvae and Odonata nymphs) were also important components of biomass intake (Table 1 and Fig. 1).

2) Little Egret

Little Egret chicks consumed 18 types of prey, which amounted to 1,237 items in 27 regurgitated boluses. Insects were the most important items numerically, while fish were the most important by dry mass (Table 1). Fish were also a numerically important prey category for Little Egret chicks. Odonata were the most frequent insect prey for Little Egret chicks, contributing 49.9% of prey items and 71.7% of dry mass, followed by Coleoptera (45.8% of prey items and 25.3% of dry mass) (Fig. 1).

3) Cattle Egret

We identified 19 types of prey among 2,377 prey items in 18 boluses produced by Cattle Egret chicks. Insects were the most important component of prey provided to Cattle Egret chicks, both numerically and by dry mass (Table 1). Spiders were also important prey (19.6% of prey items and 16.4% of dry mass) and frogs were important food items for Cattle Egret chicks by dry mass (27.1%). Orthoptera (grasshoppers, 39.6%) were the most frequent insect prey, followed by Odonata (28.0%) and Coleoptera (27.2%) (Fig. 1). On a mass basis, Odonata were the most important category (54.7%), followed by Coleoptera (21.5%) and Orthoptera (20.3%).

4) Habitat type

Intermediate Egrets mainly foraged in rice fields to acquire food for their nestlings (Table 2), but prey from grasslands and freshwater habitats was also occasionally obtained. Rice paddies contributed more to the diet of Little Egret nestlings (Table 2), but prey from freshwater habitats was also important. Rice paddies and grasslands were the sources of the food provided to Cattle Egret chicks. We found no prey items from freshwater habitats in the diet of Cattle Egret nestlings.

5) Interspecific comparison

Although insects and fish were consumed by each of the three ardeid species, there were interspecific differences in the composition of the nestlings' diet. Fish (especially Loaches *Misgurnus sp*.) were included in most regurgitated boluses of Intermediate and Little Egrets (Table 1), but other fish species were also present in Little Egret boluses (Appendix). Fish contributed most to the biomass of the Intermediate and Little Egret diet, while insects were the largest component by mass in the Cattle Egret diet (Table 1). Little Egrets also consumed more amphibians and crustaceans than the other two species. Five Little Egret boluses contained small bivalves, but bivalves were absent from Intermediate and Cattle egret boluses. Compared with other egret species Cattle Egrets consumed more spiders and grasshoppers (Table 1 and Fig. 1); spiders were included in all regurgitated boluses of Cattle Egrets, while only 45.8% and 11.1% of boluses of Intermediate and Little Egrets, respectively, contained spiders. Among insect prey, Intermediate and Little Egrets fed mainly on Coleoptera and Odonata, while Cattle Egrets fed on these taxa, but also frequently consumed Orthoptera (Fig. 1).

Cattle Egrets ate many more types of prey than the other species, which resulted in a significantly higher estimate of dietary diversity (Table 3). The average number of prey types contained in each nest sample was greater in Cattle Egrets (Kruskal–Wallis test, $H_2=15.354$, $P<0.001$) and prey diversity in the diet of Cattle Egret nestlings was significantly

Table 2. Percentage (%) of the diet obtained from each of three habitat types for three egret species.

Habitat type	Abundance			Biomass		
	Intermediate Egret	Little Egret	Cattle Egret	Intermediate Egret	Little Egret	Cattle Egret
Freshwater	0.2	11.9	0.0	1.7	27.2	0.0
Rice paddy	91.4	81.8	36.2	93.6	70.8	62.8
Grasslands	8.4	6.3	63.8	4.7	2.0	37.2
Total	1,268	1,237	2,377	89.4 g	90.7 g	78.0 g

Table 3. Comparison of trophic diversity of nestling diets among three egret species. Values are means ± SE.

Species	No. of prey types	Diversity	Evenness
Intermediate Egret	5.04 ± 1.46^{b}	0.97 ± 0.37^{b}	0.63 ± 0.22^{b}
Little Egret	4.89 ± 2.29^{b}	1.12 ± 0.42^{ab}	0.78 ± 0.13^{a}
Cattle Egret	7.78 ± 2.41^{a}	1.32 ± 0.30^{a}	0.68 ± 0.17^{ab}
Statistics*	$H_2=15.354$ $P<0.001$	$H_2=8.603$ $P<0.05$	$H_2=7.487$ $P<0.05$

*Kruskal–Wallis test. Values with the same superscript letter were not significantly different based on Dunn's multiple comparisons tests.

Table 4. Interspecific overlap in abundance and biomass composition by prey type in the diets of three egret species as measured by Schoener's Similarity Index (SSI).

Species		Diet overlap (SSI)
Intermediate Egret vs. Little Egret	Abundance	0.512
	Biomass	0.625
Little Egret vs. Cattle Egret	Abundance	0.421
	Biomass	0.267
Intermediate Egret vs. Cattle Egret	Abundance	0.426
	Biomass	0.319

greater than that of the other species ($H_2=8.603$, $P<0.05$). Intermediate Egrets ate larger loach specimens (median=56 mm, n=119) and a wider size range (20–135 mm) than the other species; Cattle Egrets (median=42 mm, range=29–65 mm, N=382) ate larger fish than Little Egrets (median=33 mm, range=20–95 mm, N=57), although Little Egrets fed on a wider size range of loaches.

The three egret species showed partial overlap in nestling prey items (Table 4). Based on both prey taxa and biomass, the strongest similarity in diet was found between Little Egrets and Intermediate Egrets (Table 4). Cattle Egrets had low similarity values with the other two species and even lower similarity based on biomass (Table 4).

DISCUSSION

This study showed that fish, especially loaches, and aquatic insects were the most important prey items in the diets of Intermediate and Little Egret nestlings, and that aquatic and terrestrial invertebrates were major prey for Cattle Egret nestlings. The high proportion of loaches and aquatic insect larvae (mainly Odonata and Coleoptera) in the diets of egret nestlings was probably related to adult birds feeding in rice fields.

Rice field ecosystems are composed of various microhabitats, including the paddy areas, terrestrial and grassy banks (levees), ditches, and irrigation channels, and these contrasting microhabitats support biodiversity, including numerous water bird species worldwide (Fasola & Ruiz 1996; Stafford et al. 2010). Fields that are temporarily flooded during the rice-growing season provide especially good habitat for several aquatic organisms. For example, in spring, the flooded fields provide spawning habitat for loaches and frogs, and several species of dragonflies and water beetles prefer shallow flooded fields for the juvenile period (Lane & Fujioka 1998; Han et al. 2010). Terrestrial invertebrates (spiders and orthopterans, such as locusts and grasshoppers) are abundant on the grassy levees between flooded rice fields (Lane & Fujioka 1998; Han et al. 2010).

Most heron species prefer natural marshes to rice fields for feeding (Tourenq et al. 2001; Kushlan & Hancock 2005). As natural wetland habitats decrease, however, rice fields provide an alternative feeding habitat for species that forage in shallow water (Fasola & Ruiz 1996). Sato and Maruyama (1996) found that Intermediate Egrets preferred flooded rice fields to rivers or dry fields for feeding and we also found that Intermediate Egrets are highly dependent on rice fields during the breeding season (Choi et al. 2007). The high concentrations of egrets commonly observed in flooded fields may be attributable to high prey abundance and ease of foraging (Sato & Maruyama 1996). Rivers are too deep for some egret species to forage, and prey are relatively scarce in dry fields compared with flooded fields. Flooded rice fields having shallow water may be well suited for egret foraging until the rice crop becomes tall and dense.

We found some differences in the proportion of each prey type taken among the species. These differences may be related to differences in foraging sites and distribution of preferred prey among species (Miranda & Collazo 1997; Smith 1997; Olmos et al. 2001; Martínez 2004; Jakubas & Mioduszewska 2005; Kazantzidis & Goutner 2005). The dietary composition of Intermediate Egret nestlings was more similar to that of Little Egrets than to that of Cattle Egret nestlings. Although both Intermediate and Cattle egrets primarily foraged in rice fields, the

similarity of their nestlings' diets was lower than expected. Intermediate Egrets foraged mainly on aquatic insects and loaches in flooded fields, whereas Cattle Egrets frequently consumed terrestrial prey, such as spiders and orthopterans, as well as aquatic insects. The high frequency of terrestrial prey in the Cattle Egrets' diet indicates that this species foraged frequently on grassy levees between flooded fields or captured prey selectively from within flooded fields. Choi et al. (2010) previously reported that Cattle Egrets mainly captured small insect prey in flooded fields, but that Intermediate Egrets often caught loaches as well as insects. When the rice crop grows rapidly in height and density (in June), thereby precluding egrets from foraging, both species increase their use of levees in their search for prey (Choi et al. 2007). During periods when rice fields are densely vegetated, levees provide gaps in vegetation suitable for herons foraging on aquatic prey at the edges of fields (Sato & Maruyama 1996; Maeda 2001; Choi et al. 2007). Although both species foraged on grassy levees, Cattle Egrets caught prey on grassy levees while Intermediate Egrets foraged more frequently at field boundaries or in small ditches near levees (Yu-Seong Choi and Hyung-Kyu Nam unpublished data). Little Egrets were more distinct, although loaches and aquatic insect larvae made up large proportions of their diet, they consumed many other freshwater fish (e.g., Topmouth Gudgeon *Pseudorasbora parva*, and Goby Minnow *Pseudogobio esocinus*) and shrimp (*Caridina denticulata*), which are rare in rice fields. This suggests that this species foraged in other freshwater habitats such as reservoirs and streams, as well as in rice fields. Little Egrets can forage in all available feeding habitats, which may account for the large variation in their prey (Kazantzidis & Goutner 2005). The Little Egret may have a special ability to find sites in which prey is temporarily abundant (Kushlan & Hancock 2005), as this species is highly opportunistic in selecting feeding sites and prey.

In conclusion, we showed that three egret species foraged mainly in rice fields, which represented the most extensive habitat surrounding their breeding colony, and none of the egrets showed a clear preference for particular prey. Some dietary segregation was observed between the three ardeid species in terms of relative frequency and biomass of prey items, and it is suggested that food resource partitioning was occurring among the species.

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Appendix. The frequency of occurrence, number of prey items, and dry mass of each prey type identified in regurgitated boluses of Intermediate Egret, Little Egret, and Cattle Egret nestlings.

Egret species / Prey type	Intermediate Egrets						Little Egrets						Cattle Egrets					
	Bolus	%	Item	%	Mass	%	Bolus	%	Item	%	Mass	%	Bolus	%	Item	%	Mass	%
Pisces																		
Misgurnus sp.	20	83.3	119	9.4	51.0	57.0	24	88.9	382	30.9	38.0	41.9	6	33.3	57	2.4	6.0	7.7
Monopterus albus	1	4.2	3	<1.0	5.1	5.8	5	18.5	18	1.5	11.9	13.1	–	–	–	–	–	–
Pseudorasbora parva	1	4.2	2	<1.0	1.5	1.7	6	22.2	10	<1.0	5.6	6.2	–	–	–	–	–	–
Pseudogobio esocinus	–	–	–	–	–	–	1	3.7	1	<1.0	2.7	3.0	–	–	–	–	–	–
Amphibia																		
Frogs	2	8.3	2	<1.0	1.9	2.2	1	3.7	1	<1.0	0.9	1.0	10	55.6	15	<1.0	20.6	26.4
Tadpoles	3	12.5	9	<1.0	0.7	0.8	14	51.9	134	10.8	10.8	11.9	2	11.1	7	<1.0	0.6	0.7
Bivalvia																		
Freshwater bivalves	–	–	–	–	–	–	5	18.5	40	3.2	0.2	0.3	–	–	–	–	–	–
Malacostraca (Crustacean)																		
Atyidae	1	4.2	1	<1.0	<0.1	<0.1	6	22.2	78	6.3	4.3	4.7	–	–	–	–	–	–
Arachnida																		
Spiders	11	45.8	29	2.3	0.8	0.9	3	11.1	6	<1.0	0.2	0.2	18	100.0	465	19.6	12.8	16.4
Insecta																		
Lepidoptera im.[#]	–	–	–	–	–	–	–	–	–	–	–	–	2	11.1	2	<1.0	<0.1	<0.1
Lepidoptera la[#].	2	8.3	2	<1.0	<0.1	<0.1	–	–	–	–	–	–	7	38.9	36	1.5	0.6	0.8
Hemiptera (te.)[#]	–	–	–	–	–	–	–	–	–	–	–	–	1	5.6	1	<1.0	<0.1	<0.1
Hemiptera (aq.)[#]	6	25.0	12	<1.0	0.3	0.3	4	14.8	18	1.5	0.4	0.5	6	33.3	8	<1.0	0.2	0.2
Orthoptera	11	45.8	21	1.7	2.0	2.2	1	3.7	2	<1.0	<0.1	<0.1	15	83.3	724	30.5	7.6	9.7
Coleoptera (aq.) im.[#]	5	20.8	40	3.2	0.9	1.0	2	7.4	2	<1.0	<0.1	<0.1	1	5.6	1	<1.0	<0.1	<0.1
Coleoptera (aq.) la.[#]	22	91.7	727	57.3	12.7	14.2	13	48.1	196	15.8	2.8	3.1	16	88.9	367	15.4	5.2	6.7
Coleoptera (te.) im.[#]	5	20.8	24	1.9	0.5	0.6	12	44.4	48	3.9	1.0	1.1	16	88.9	130	5.5	2.8	3.6
Odonata im.[#]	6	25.0	24	1.9	0.8	0.9	10	37.0	19	1.5	0.6	0.6	12	66.7	106	4.5	3.6	4.6
Odonata la.[#]	18	75.0	244	19.2	10.1	11.3	20	74.1	249	20.1	10.4	11.5	10	55.6	406	17.1	16.8	21.6
Diptera	3	12.5	4	<1.0	<0.1	<0.1	3	11.1	3	<1.0	<0.1	<0.1	13	72.2	45	1.9	0.4	0.6
Blattodea	–	–	–	–	–	–	–	–	–	–	–	–	1	5.6	1	<1.0	<0.1	<0.1
Unidentified	1	4.2	2	<1.0	<0.1	<0.1	–	–	–	–	–	–	1	5.6	1	<1.0	<0.1	<0.1
Annelida																		
Earthworms or leeches	3	12.5	3	<1.0	1.0	1.1	2	7.4	30	2.4	0.9	1.0	2	11.1	2	<1.0	0.7	0.8
Others	–	–	–	–	–	–	–	–	–	–	–	–	1	5.6	3	<1.0	<0.1	<0.1
Total	24		1,268		89.4		27		1,237		90.7		18		2,377		78.0	

[#] im., imagoes; la., larvae; aq., aquatic; te., terrestrial.