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The freshwater grass shrimp *Palaemonetes antennarius* in the diet of fish in Lake Bracciano (Central Italy)

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Abstract – We evaluated the importance of the freshwater grass shrimp *Palaemonetes antennarius* as trophic source for the lacustrine fish of the Lake Bracciano (Central Italy) analyzing 6120 stomach contents of 10 species. Shrimp was recorded for all size classes of the investigated species with a variation in frequency and abundance depending on seasons. *P. antennarius* was occasionally preyed by cyprinids, and systematically by small individuals of carnivorous fish. Our findings acquire more importance if we take the shrimps ecological niche into account, as it is potentially acting as detritivorous/generalist and predator of benthic invertebrates as well. This feeding behavior makes *P. antennarius* an important network ring, being a taxon that ought to receive the same attention recommended for other freshwater decapods as proposed for *Austropotamobius pallipes* and *Potamon fluviatile*.

Key-words: Decapoda / Palaemonidae / *Palaemonetes antennarius* / fish stomach content analysis / Mediterranean

Résumé – La crevette d'eau douce *Palaemonetes antennarius* dans l'alimentation des poissons du lac de Bracciano (Italie centrale). Nous avons évalué l'importance de la crevette d'eau douce *Palaemonetes antennarius* comme source trophique pour les poissons lacustres du lac de Bracciano (Italie centrale) par analyse de 6120 contenus stomacaux de 10 espèces. La crevette a été trouvée pour toutes les classes de taille des espèces étudiées avec une variation de la fréquence et de l'abondance en fonction des saisons. *P. Antennarius* a été consommée occasionnellement par les cyprinidés, et systématiquement les petits individus des poissons carnivores. Nos résultats acquièrent plus d'importance si nous prenons la niche écologique des crevettes en compte, car elle agit potentiellement comme détritivore/généraliste et également prédateur d'invertébrés benthiques. Ce comportement alimentaire fait de *P. antennarius* un important nœud du réseau trophique, et un taxon qui devrait recevoir la même attention que celle recommandée pour les autres décapodes d'eau douce comme *Austropotamobius pallipes* et *Potamon fluviatile*.

Mots-clés : Decapode / Palaemonidae / Palaemonetes antennarius / contenu stomacal / Méditerranéen

Although scientists are aware that every singular species is the result of biological interactions with other taxa within an ecological network (*e.g.* Allesina and Pascual, 2009), conservation efforts still persevere in focusing on a single or a modest number of species displaying relevant roles within an ecosystem (Okey, 2004; Jordán *et al.*, 2009). This is due to the prevailing opinion that only particular groups are expected to play an important role but ecological network interactions among the single species and the community dynamics have largely been ignored (Stouffer *et al.*, 2012). Nowadays the current challenge is to quantify the relative importance of a single species in an ecosystem, assuming that the well-linked species are important for the whole community (Jordán, 2009). Though it is not always simple to define the sense of "important" from an ecological point of view, Kearns *et al.* (1998) defined important those species having the major number of links with other taxa. Theoretically this means that functionally important species could be those occupying central positions in the ecological network (Allesina and Bodini, 2004). For this reason, one approach in describing the importance of keystone species in the whole food web (Jordán *et al.*, 2008) is to characterize the trophic aggregation of ecological groups in order to describe the interactors having a greater role within the community (Estrada, 2007; Jordán *et al.*, 2007).

Based on these premises, the main purpose of this study is to highlight the importance of the freshwater grass shrimp *Palaemonetes antennarius* (Milne Edwards, 1837) in the diet of fish species inhabiting the volcanic Lake Bracciano (Central Italy). This grass shrimp, recently proposed as junior synonyms of *Palaemon* Weber, 1795 (De Grave and Ashelby, 2013), is a caridoid body shaped southern Europe decapod belonging to the family Palaemonidae Gottstein Matoèec and

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Table 1. Fish check-list of the Lake Bracciano (Gibertini *et al.*, 2004). The years of investigation are indicated for each studied species in the last column.

Family		Species	Authority	Year
Anguillidae	1	*Anguilla anguilla*	(Linnaeus, 1758)	1994
Atherinidae	2	*Atherina boyeri*	(Risso, 1810)	1994, 2003
Blennidae	3	*Salaria fluviatilis*	(Asso, 1801)	
Centrarchidae	4	*Lepomis gibbosus*	(Linnaeus, 1758)	2003, 2008
	5	*Micropterus salmoides*	(Lacépède, 1802)	2003, 2008
Cyprinidae	6	*Alburnus alburnus alborella*	(De Filippi, 1844)	
	7	*Barbus plebejus*	(Bonaparte, 1839)	
	8	*Carassius carassius*	(Linnaeus, 1758)	
	9	*Cobitis taenia bilineata*	(Canestrini, 1865)	
	10	*Cyprinus carpio*	(Linnaeus, 1758)	1992, 1999
	11	*Squalius cephalus*	(Linnaeus, 1758)	
	12	*Rutilus rubilio*	(Bonaparte, 1837)	2003, 2008
	13	*Scardinius erythrophthalmus*	(Linnaeus, 1758)	
	14	*Tinca tinca*	(Linnaeus, 1758)	1994, 2003
	15	*Telestes muticellus*	(Bonaparte, 1837)	
Esocidae	16	*Esox lucius*	(Linnaeus, 1758)	1992, 1994, 2003
Gobidae	17	*Padogobius bonelli*	(Bonaparte 1846)	
	18	*Padogobius nigricans*	(Canestrini, 1867)	
Ictaluridae	19	*Ictalurus punctatus*	(Rafanisque, 1818)	
Mugilidae	20	*Liza ramada*	(Risso, 1826)	
	21	*Mugil cephalus*	(Linnaeus, 1758)	
Percidae	22	*Perca fluviatilis*	(Linnaeus, 1758)	1992, 1999
Poecilidae	23	*Gambusia holbrooki*	(Girard, 1859)	
Salmonidae	24	*Coregonus lavaretus*	(Linnaeus, 1758)	1992, 1994, 1999, 2003, 2008

Kerovec (2002) proposed it as a very rare and endangered shrimp, although the species is listed as Least Concern by the International Union for Conservation of Nature (http://www.iucnredlist.org). Although investigations on behavior (Ugolini *et al.*, 1988, 1989; Ungherese *et al.*, 2008) and ecology of *P. antennarius* are performed at local level (Dalla Via, 1983; Gottstein Matoèec *et al.*, 2006) some ecological aspects, such as interspecific relationships with predators or other taxa of the food web remain still unclear.

To reach our goal we analysed 6120 individuals of 10 different fish species (Table 1) caught every January, April, July, and October of 1992, 1994, 1999, 2003, and 2008, for histological investigations concerning reproductive aspects (both gonado- and gametogenesis). Fish sampling was supported by professional fishermen which collocated 6 dragnets having a 2 cm mesh-size, in 6 different sites in the south-eastern lake area covering nearby 4 km^2 of the 57.2 km^2 water surface. Nets were fixed during sunset and drawn in the morning after. The catch per unit effort was the same in each season for the 5 years, with the exception of 2003 and 2008 when dragnets were landed using a motor-driven winch. In every sampling session, 10–15 specimens per species were selected and measured on their right body side from the mouth tip to the caudal peduncle (standard length, SL, in cm) Stomachs were collected, preserved in 85° alcohol, and sorted in laboratory. All intact or remnants of *P. antennarius* were divided per sampling season and year, species, and fish body size (using 5 cm SL range). We firstly calculated the grass shrimp occurrence frequency as $O = (J_i/N)$, and the prey-specific abundance as $A = (\Sigma S_i/\Sigma St_i)$, where: Ji was the stomach number containing shrimps; N the number of stomachs containing preys; S_i indicated the number of shrimps in the stomachs; St_i the total preys in the stomachs containing shrimps. To assess how *P. antennarius* influences the fish diet strategy, both O and A (for species and year) were plotted in a series of diagrams (Amundsen *et al.*, 1996). The analysis is based on a graphical exploration of the ingested food in relation to the predator feeding strategy, as well as the intra- and inter-individual shifts in the niche use. Specifically, in this graph data plotting follows three main directions (Supplementary Material 1): the first diagonal represents the prey abundance within the predator diet spectrum; the second, parallel to the y-axis, provides information on the predator specialization for the specific prey; the third diagonal refers to the individual resource use. The latter changing from 'high between individuals' (HBI, that means how many specimens of a specific predator consume shrimps, but the latter is no very abundant within each stomach) to 'high within individuals' (HWI, that means not many specimens of a specific predator feed on shrimps, but the latter is abundant within the stomach).

Additionally we evaluated the shrimp body size by extrapolating it from the regression functions calculated for 200 specimens collected from Lake Bracciano. We performed the same measurements as Anastasiadou *et al.* (2009) using a digital caliper (± 0.01 mm), and considered the cephalothorax length (CTL) as the reference size. Although authors are aware that *P. antennarius* shows a morphometric sexual dimorphism pattern (see Anastasiadou *et al.*, 2009), we chose to perform

Table 2. Shrimp occurrence within full stomachs, divided per sampling season and year, and standard length range (SL, cm) of the 10 investigated species (au = autumn; wi = winter; sp = spring; su = summer).

	SL	1992				1994				1999				2003				2008			
	(cm)	au	wi	sp	su	au	wi	sp	su	au	wi	sp	su	au	wi	sp	Su	au	wi	sp	su
A. anguilla	25–30					0.14	0.20	0.11	0.20												
	30–35					0.14	0.13	0.20	0.17												
	35–40					0.20	0.18	0.17	0.14												
	40–45					0.13	0.20	0.22	0.14												
	45–50					0.11	0.25	0.25	0.25												
A. boyeri	0–5					0.50	–	–	0.67					0.56	–	–	0.50				
	5–10					0.17	0.21	0.20	0.18					0.21	0.15	0.20	0.18				
C. lavaretus	5–10	0.25	–	–	0.25	0.40	–	–	0.25	0.33	–	–	0.33	0.50	–	–	0.33	0.50	–	–	0.33
	10–15	–	–	–	0.08	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	15–20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	–	–	–
	20–25	–	–	0.09	–	–	–	–	–	0.10	–	–	–	–	–	–	–	–	–	–	–
	25–30	0.08	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08	–	–	–
E. lucius	10–15	0.25	0.17	0.25	–	0.20	–	0.25	0.17					–	0.20	0.33	0.14				
	15–20	0.38	0.43	0.44	0.40	0.38	0.38	0.43	0.33					0.33	0.25	0.33	0.43				
	20–25	0.25	0.40	0.27	0.25	0.33	0.43	0.27	0.33					0.22	0.27	0.25	0.13				
	25–30	0.25	0.22	0.23	0.25	0.40	0.14	0.27	0.18					0.15	0.14	0.40	0.25				
	30–35	0.30	0.27	–	0.29	0.33	–	0.20	0.33					0.27	0.38	0.33	0.25				
	35–40	–	–	–	–	–	–	0.09	–					–	–	–	–				
	40–45	–	–	–	–	–	–	–	–					–	–	–	–				
	45–50	–	0.11	–	–	–	–	–	–					–	–	0.09	–				
P. fluviatilis	5–10	0.25	–	0.29	0.25					0.17	–	0.17	0.14								
	10–15	0.13	0.17	–	0.17					0.29	0.25	0.20	0.29								
	15–20	0.27	0.22	0.23	0.27					0.36	0.22	0.25	0.27								
	20–25	0.40	0.25	0.38	0.27					–	0.17	–	0.22								
	25–30	0.40	0.46	0.40	0.43					0.38	0.36	0.30	0.38								
	30–35	0.27	0.38	0.31	0.33					0.33	0.63	0.20	0.25								
	35–40	0.45	0.42	0.56	0.36					0.33	0.27	0.36	0.36								
M. salmoides	5–10													0.67	0.50	0.50	0.67	0.50	0.50	0.60	0.67
	10–15													0.44	0.40	0.43	0.44	0.50	0.50	0.38	0.43
	15–20													0.20	0.14	0.25	0.18	0.21	0.20	0.23	0.18
	20–25													0.30	0.43	0.57	0.22	0.43	0.33	0.50	0.18
	25–30													0.22	0.20	0.22	0.18	0.25	0.20	0.22	0.22
C. carpio	10–15	0.17	0.14	–	0.17					0.14	0.20	–	0.25								
	15–20	0.13	0.18	0.13	0.20					0.13	0.10	0.17	0.14								
	20–25	0.18	–	0.08	0.14					0.18	0.25	0.20	0.11								
	25–30	0.11	0.10	–	0.18					0.20	0.14	0.13	0.11								
	30–35	–	0.10	0.09	0.13					0.14	0.11	–	0.10								
	35–40	0.13	0.17	0.22	0.13					–	0.11	0.13	0.14								
L. gibbosus	5–10													0.17	–	0.17	–	–	0.14	0.17	–
	10–15													0.23	0.17	0.20	0.15	0.21	0.18	0.22	0.17
	15–20													0.38	0.38	0.40	0.36	0.33	0.38	0.40	0.33
R. rubilio	0–5													0.25	–	–	0.14	–	–	0.17	–
	5–10													–	0.20	0.14	–	0.20	–	0.25	0.17
	10–15													0.07	–	0.10	–	0.10	0.09	0.09	–
	15–20													0.11	0.10	–	0.09	0.13	–	0.08	0.13
T. tinca	5–10					0.20	0.14	0.10	–					–	0.14	0.14	–				
	10–15					–	0.25	–	–					0.13	0.11	–	0.33				
	15–20					0.10	–	0.09	–					–	0.10	0.09	0.13				
	20–25					–	–	0.13	0.09					0.09	–	0.14	–				
	25–30					0.08	0.11	–	0.08					–	–	–	0.14				
	30–35					–	0.11	–	0.09					0.13	–	–	0.11				
	35–40					–	–	0.09	–					0.09	–	0.13	–				

a series of regression for the entire sample since we were not able to sex all grass shrimp remnants within stomachs. Then we regressed shrimp size *vs.* fish size in order to observe eventual preferences in the choice of prey size.

Our outputs support the hypothesis that the freshwater grass shrimp plays a relevant role in fish diet. In fact, *P. antennarius* occurred inside stomachs of all investigated fish species, although in different frequencies and life stages (larval, sub-adult, and adult, the latter being the most exploited by fish). Moreover, its occurrence depended on fish size and seasons as well. On the whole 4295 stomachs (70.18%) showed animal contents and 635 (15.8%) contained entire grass shrimp bodies or remnants. Shrimps occurred only as larval form in planktonfagous species such as *Coregonus lavaretus* (Linnaeus, 1758) and *Atherina boyeri* (Risso, 1810) in summer and autumn, when juvenile individuals of both fish species reside near the riparian shore of the lake (Avetrani *et al.*, 2006). In the remaining 8 fish species, sub-adult and/or adult of shrimps were the most preyed life stage and occurred in stomachs of all size classes with the only exception of the *Esox lucius* 40–45 cm class . Additionally *P. antennarius* was easily recorded in predators (mainly in small sized specimens) such as *E. lucius* Linnaeus, 1758, *Micropterus salmoides* (Lacépède, 1802), and *Perca fluviatilis* Linnaeus, 1758 (see also Marinelli *et al.*, 2007; Scalici *et al.*, 2009a; Godinho and Ferreira, 2014). Generally, the occurrence frequency (Table 2) showed a wide value range for the entire sample having a minimum of 0.08 for the diverse species and a maximum of 0.67

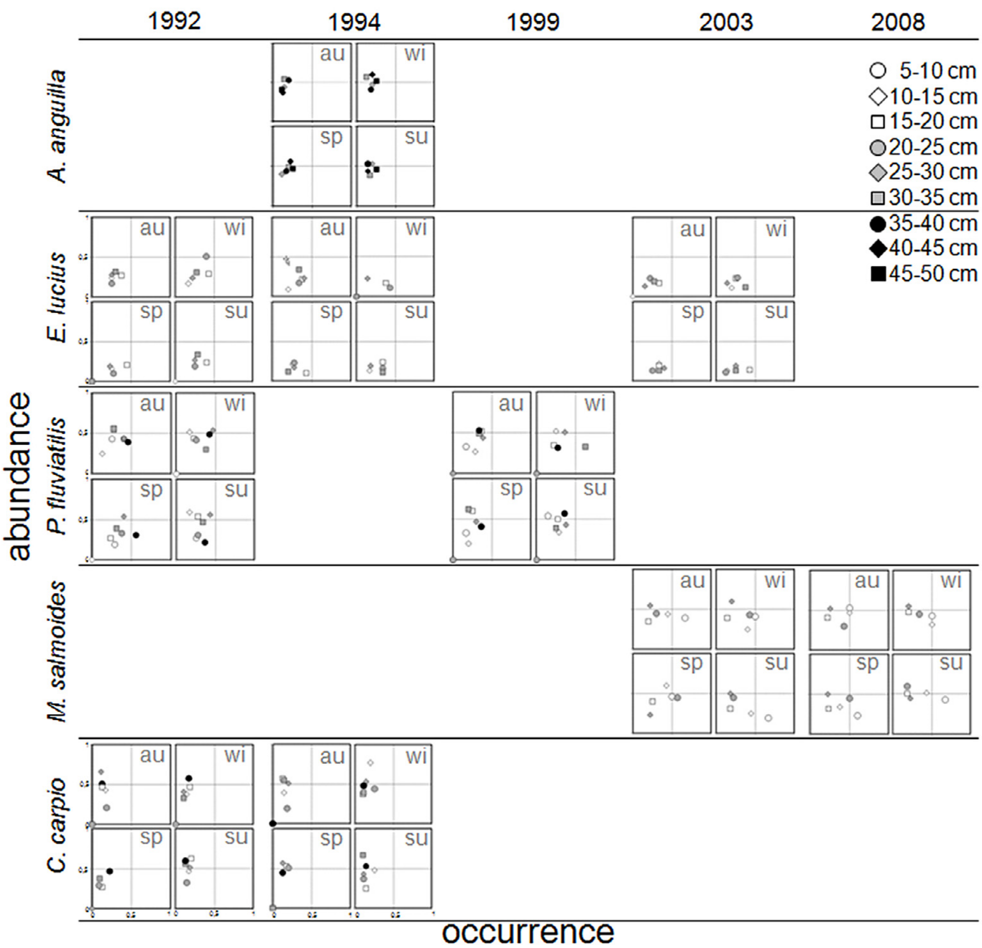

Fig. 1. Alimentary diagrams obtained plotting both freshwater shrimp abundance and occurrence for 5 selected species divided per sampling season (au = autumn; wi = winter; sp = spring; su = summer) and year, and standard length range in cm. The remaining fish species showing few data or an occasional occurrence of *P. antennarius* were excluded in this analysis. Since we would not evaluate fish species diet overlap, only the shrimp components found inside the stomachs were shown in the Amundsen *et al.* (1996) graphic outputs.

for *A. boyeri* and *M. salmoides*. The Amundsen *et al.* (1996) method was applied only to 5 selected species (Figure 1). In several diagrams *P. antennarius* is under the O value of 0.5, with the exception of *M. salmoides*, indicating that the crustacean is preyed mostly by fish displaying a generalized feeding strategy. All fish species mainly fed on adult shrimp (Figure 2), referring to near CTL = 12 mm as size at maturity according to Gottstein Matoèec *et al.* (2006). Although in regressing shrimp size *vs.* fish size some significant outcomes emerged, overall for *P. fluviatilis* and *M. salmoides*, which always showed significant regressions (Table 3). Some regressions seemed to be casual for certain species. For example, the analysis provided significant outcomes for pike during the first sampling year, but not for the following ones. On the other hand, when the standard length of both *P. fluviatilis* and *M. salmoides* increased also the size of ingested shrimps increased.

Taking the double role of prey for fish and possible predator of benthic invertebrates into account (Cibinetto *et al.*, 2005), the freshwater grass shrimp position in the food web brought to mind that it is of crucial importance as intermediate trophic species in 'wasp-waist' ecosystems The latter are typical for pelagic upwelling areas (Cury *et al.*, 2000) where a large number of taxa are linked by a single or only very few species collocated in the middle of the trophic levels (Smith Jr *et al.*, 2007). This 'centrality' makes *P. antennarius* a more imperiled taxon if we also consider the introduction and spreading of both alien invertebrates and fish species as potential competitors and/or predators This may be the case for very stressed areas such as in central Italy where diverse invasive crayfish (Chiesa *et al.*, 2006; Nonnis *et al.*, 2009; Scalici *et al.*, 2010, 2009b, 2009c; Dörr and Scalici, 2013; Bissattini *et al.*, accepted) and their unsafe parasites (Dörr *et al.*, 2011, 2012a, 2012b; Chiesa *et al.*, 2015) were recorded and described. Scientists are often expected to indicate the most important species which disturbance may originate the main detrimental effect on both occurrence and abundance of other taxa in a community (Jones *et al.*, 1994). From this viewpoint, *P. antennarius* ought to receive the same attention recommended for other freshwater decapods (see Brusconi *et al.*, 2008) as proposed for *Austropotamobius pallipes* species complex *sensu* Chiesa *et al.* (2011) and Scalici and Bravi (2012) (see http://www.iucnredlist.org) or suggested for *Potamon fluviatile* (Herbst, 1785) (see Jesse *et al.*, 2009). Nevertheless, the

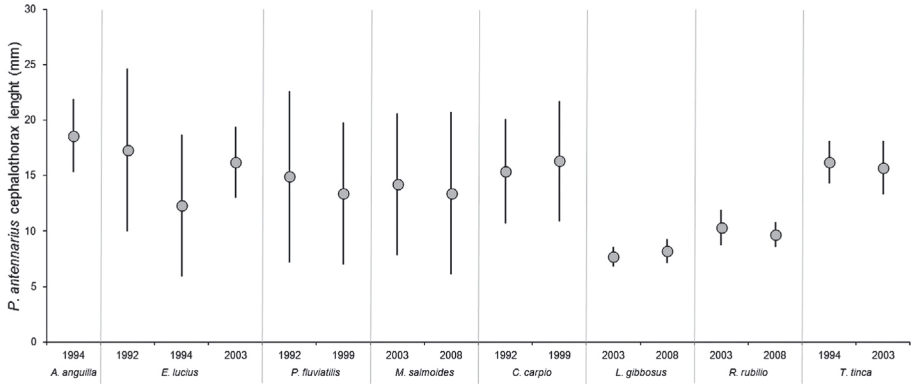

Fig. 2. *P. antennarius* cephalothorax mean length (CTL, ± standard deviation) for the 8 selected and investigated species divided per sampling year.

Table 3. Correlations between *P. antennarius* cephalothorax length (CTL) and fish standard length of the 8 selected species divided per sampling year (significant values are in bold; ns = not significant). The two planktofagous species *C. lavaretus* and *A. boyeri* were omitted from the analysis, since no data on shrimp larval size and growth were available.

	1992		1994		1999		2003		2008	
CTL *vs.* size of	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*
A. anguilla			0.507	ns						
E. lucius	0.684	<0.05	0.499	ns			0.339	ns		
P. fluviatilis	0.843	<0.01			0.903	<0.01				
M. salmoides							0.891	<0.01	0.911	<0.01
C. carpio	0.699	<0.05			0.526	ns				
L. gibbosus							0.571	ns	0.308	ns
R. rubilio							0.377	ns	0.349	ns
T. tinca			0.714	<0.05			0.562	ns		

significant role of the freshwater grass shrimp and the dynamic consequences due to its presence need to be confirmed, since understanding the dynamic implications of a species role in the food web may provide useful information when scientists have to dialogue with institutions for deciding which taxa is of main concern in conservation and managing efforts, and to focalize on those with the strongest involvement in community persistence.

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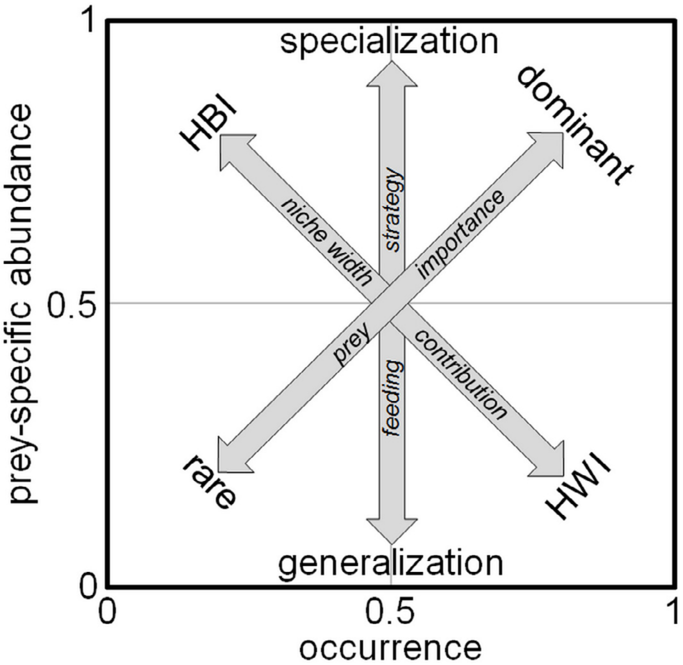

Supplementary Material 1. Graphic representation for the interpretation of feeding strategy, niche width contribution, and prey importance, as proposed by Amundsen *et al.* (1996) (figure modified). HBI = high between individuals; HWI = high within individuals.