

FEEDING HABITS OF SYMPATRIC *DISCOGLOSSUS MONTALENTII*, *DISCOGLOSSUS SARDUS* AND *EUPROCTUS MONTANUS* DURING THE BREEDING SEASON

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The diets of three Corsican amphibians, *Discoglossus montalentii*, *Discoglossus sardus* and *Euproctus montanus*, were studied in the Ospedale region during the breeding season. Adult specimens were collected in or around breeding pools and were stomach flushed in the field. Prey taxa included a large variety of terrestrial and aquatic prey items of variable size, indicating opportunistic predation. All species were able to catch their prey both on land and in water, but varied in the proportions of aquatic and terrestrial prey consumed. *E. montanus* fed largely upon benthic macroinvertebrates, suggesting predation in deep water; *D. sardus* mainly captured terrestrial prey; and *D. montalentii* showed a mixed feeding strategy, preying upon both terrestrial and aquatic prey categories in similar proportions. *Discoglossus sardus* showed the highest standardized value of niche breadth ($D_s = 0.769$), compared to *D. montalentii* and *E. montanus* ($D_s = 0.544$ and $D_s = 0.523$ respectively). When prey size frequency distributions were compared, no specific differences were observed. These results indicated that, at least during the breeding season, trophic segregation among sympatric amphibians was maintained by different foraging strategies, and that the three species exploited contiguous microhabitats in different ways.

Key words: Corsica, *Discoglossus*, *Euproctus*, foraging strategy, sympatry

INTRODUCTION

On the Mediterranean island of Corsica seven amphibian species, including three endemic forms (*Euproctus montanus*, *Discoglossus montalentii* and *Salamandra corsica*), are known to occur (Delaugerre & Cheylan, 1992; Gasc *et al.*, 1997). The Corsican painted frog *D. montalentii* was the last species to have been described on the basis of biochemical and morphological characters (Lanza *et al.*, 1984), and -due to its confusion with the congeneric Tyrrhenian painted frog *D. sardus* - little is known about its biology and ecology. *Discoglossus montalentii* is mainly a mountain species living in pristine or semi-pristine forest streams, while *D. sardus* breeds from sea level to about 1300 m, in a variety of aquatic habitat types (Clark & Lanza, 1990; Lanza, Vanni & Brizzi, 1992a,b). The altitudinal distribution of the two species overlaps broadly, and in several areas they are found together (Clarke & Lanza, 1990; Salvidio *et al.*, unpublished data). During a two year field study on the distribution and ecology of *D. montalentii* and *D. sardus*, we collected data on their feeding habits together with those of the sympatric Corsican brook salamander *E. montanus*. This gave us the opportunity to analyse their feeding behaviours and to compare their foraging modes in order to investigate whether they were partitioning food resources when they coexist.

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STUDY AREA AND METHODS

Samples were collected in the Ospedale forests (Southern Corsica, 20 km NW of Portovecchio) from April to June, both in 1996 and 1997. The study area, a *Pinus laricio* forest ranging from 700 to 1000 m a.s.l., was located between the villages of Ospedale and Zona, which are separated by a linear distance of about 12 km. Although very similar morphologically, *D. montalentii* and *D. sardus* were identified in the field mainly on the basis of their hindlimb length, which is relatively greater in *D. montalentii* (Clarke & Lanza, 1990; Salvidio *et al.*, unpublished data); in some cases, field identification was confirmed by dissection and by chromosomal analysis (Gaetano Odierna *in litteris*).

With the exception of *Salamandra corsica* (see below), all amphibians were captured in or near (i.e. less than 1 metre from) water. All specimens were measured from the tip of the snout to the posterior end of the vent (SVL) to the nearest mm, and toe clipped at first capture; thus, stomach contents were analyzed only once for each individual. Diet composition was obtained by stomach flushing (Fraser, 1976; Joly, 1987), and stomach contents were preserved in the field in 70% ethanol. Stomach flushing was performed at least twice on each specimen and, if no prey was obtained, the stomach was considered empty. Where possible, food items were identified to order or family, and measured to the nearest 0.1 mm under a dissecting microscope. Aquatic invertebrates were classified using Sansoni's (1988) identification keys of freshwater

macroinvertebrates. Prey volume (V) was calculated by considering each item as a cylinder or a sphere, and was expressed in mm^3 . Additionally, prey items were classified as aquatic or terrestrial, with a third category comprising prey that dwell on land, in shallow water or mud (e.g. metamorphosing anurans, mites, dipteran larvae, earthworms), as well as unidentified prey items.

Simple correspondence analysis (CA), based on a contingency table with predators as rows and prey taxa as columns, was used to obtain a graphical representation of the association between species and prey categories. In this analysis, a small sample of the Corsican fire salamander *S. corsica* (four specimens collected in the Ospedale region, and one from Haute Asco in Northern Corsica, all of them captured in terrestrial habitats) was included for comparison, as this species feeds exclusively upon terrestrial invertebrates (Kuzmin, 1994). The Corsican fire salamander sample was used in the CA as a supplementary row element; thus, it was represented in the Euclidean space determined by the first two axes, but did not contribute to the calculation of the other species location (Greenacre, 1993). Correspondence analysis was performed using Minitab 11.12 statistical software (Minitab Inc., 1996). Prey volume frequency distributions were compared with a Kolmogorov-Smirnov two sample test (Siegel & Castellan, 1988). The standardized version of Simpson's diversity index $D_s = (D - 1)/(N - 1)$, in which D is the Simpson's index ($D = 1/\sum p_i^2$) and N is the number of prey taxa categories, was used to estimate trophic niche breadth. This standardized index ranges from 0, when only one resource category is exploited, to 1 when all categories are exploited with the same frequency (Barbault, 1981).

RESULTS

During this study, 144 amphibians were stomach flushed (Table 1). The proportion of stomachs containing at least one prey item (inorganic and plant matter were excluded from data analyses) ranged from 100% in *S. corsica* to 63% in *D. sardus*, and a chi-square analysis, based on the three largest samples (i.e. excluding the *S. corsica* sample), indicated that there were no differences in the frequency of fasting animals ($\chi^2 = 4.4$, $\text{df}=2$; $P=0.108$).

The *Euproctus montanus* sample consisted of sexually mature individuals: 46 males and 6 females. The sample of *D. sardus* comprised 23 males, 6 females and 2 subadults, and that of *D. montalentii* 2 males, 13 females and 4 subadults. All subadult individuals were excluded from the quantitative data analysis. As the frequencies of terrestrial and aquatic prey categories did not differ significantly between sexes [*E. montanus* $\chi^2=0.2$, $\text{df}=1$; *D. sardus* $\chi^2=3.4$, $\text{df}=1$; *D. montalentii* $\chi^2=1.8$, $\text{df}=1$; $P>0.05$ in all cases, all tests with Yate's correction for continuity (Siegel & Castellan, 1988)], food data from males and females were combined for interspecific comparisons.

Table 2 gives the complete data set of the diet composition by taxonomic group and by volume. In the Ospedale forests, amphibians consumed a wide range of terrestrial and aquatic invertebrates. The Corsican brook salamander was the only species that preyed upon vertebrates: one unidentified urodelan larva and one postmetamorphic froglet (*Discoglossus* sp.) were found in the stomachs of two males, and a third male swallowed four eggs belonging to its own species. The distribution of prey items according to their life-style indicated that all species were able to feed both in aquatic and terrestrial environments; however, *E. montanus* fed mainly on benthic macroinvertebrates, in particular Plecoptera, Ephemeroptera and Tricoptera larvae, while *D. sardus* primarily consumed terrestrial prey (Isopoda and Araneida). *D. montalentii* captured both freshwater, and terrestrial food items in similar proportions. These results suggest that the brook salamander was foraging mainly in deep water, while the two discoglossids probably preferred surface or shallow water. The frequencies of prey according to their life-style (aquatic vs terrestrial) were overall significantly different ($\chi^2=31.3$, $\text{df}=4$, $P<0.001$), but when species were compared pairwise, the Corsican painted frog and the Corsican brook salamander showed similar feeding habits: *D. montalentii* - *E. montanus*, $\chi^2=4.9$, $\text{df}=2$; $P=0.088$; *D. montalentii* - *D. sardus*, $\chi^2=9.6$, $\text{df}=2$, $P=0.008$; *D. sardus* - *E. montanus*, $\chi^2=30.7$, $\text{df}=2$, $P<0.001$. The utilization of taxonomic categories by volume showed similar findings (Table 2), as *D. montalentii* and *E. montanus* were the species depending the most upon aquatic food resources (58% and 30% of the total ingested volume, respectively). The standardized Simpson index D_s calculated on the basis of taxonomic categories, indicated that *D. sardus* had the widest trophic niche breadth ($D_s = 0.769$), *E. montanus* the narrowest ($D_s = 0.523$), and *D. montalentii* an intermediate value ($D_s = 0.544$); but when prey volumes were considered, all species showed similar - and relatively narrow values - of niche breadths ($0.299 < D_s < 0.356$; see Table 2).

The results of the CA based on the complete data set are shown in Fig. 1. The first and second axes explained 38% and 24 % of the total variance, respectively. In this plot, both *Discoglossus sardus* and *S. corsica* were projected in the bottom right quadrant of the plot, in strict association with their terrestrial prey categories. *Discoglossus montalentii* and *E. montanus* were projected in different quadrants and their diets were characterized by swimming invertebrates (Dytiscidae and Heteroptera) and by amphibian eggs or froglets, respectively.

The analysis of prey utilization by size showed that in all species small food items ($V<9 \text{ mm}^3$) contributed a large proportion (more than 50 %) of the total number of prey, while relatively large items tended to be rather infrequent. When prey-size distributions (Fig. 2) were compared, these amphibian populations showed similar

TABLE 1. Number of stomach-flushed specimens and mean snout-vent length (SVL) of adult *D. montalentii*, *D. sardus*, *E. montanus* and *S. corsica* containing at least one prey item in the stomach.

Species	Sample size <i>N</i>	Sample with prey <i>N</i>	Adult sample with prey SVL (mm)±SD
<i>D. montalentii</i>	22	19 (86%)	44.4±9.57 (<i>N</i> = 15)
<i>D. sardus</i>	49	31 (63%)	48.4±6.27 (<i>N</i> = 29)
<i>E. montanus</i>	68	52 (76%)	49.6±3.69 (<i>N</i> = 52)
<i>S. corsica</i>	5	5 (100%)	96.6±18.04 (<i>N</i> = 5)

TABLE 2. Food composition by taxa (*N*) and by volume (*V*) expressed in mm³, and standardized trophic niche breadth (*D_s*) of *D. montalentii*, *D. sardus*, *E. montanus*, and *S. corsica*.

Prey type	<i>D. montalentii</i>		<i>D. sardus</i>		<i>E. montanus</i>		<i>S. corsica</i>	
	(15)		(29)		(52)		(5)	
	<i>N</i> (%)	<i>V</i> (%)	<i>N</i> (%)	<i>V</i> (%)	<i>N</i> (%)	<i>V</i> (%)	<i>N</i> (%)	<i>V</i> (%)
<i>Aquatic</i>								
1 Coleoptera Dytiscidae (adults)	2(5)	149(13)	-	-	-	-	-	-
2 Coleoptera (adults)-Dytiscidae excluded	6(15)	47(4)	5(8)	28(2)	2(3)	5(0)	-	-
3 Coleoptera (larvae)-Dytiscidae excluded	-	-	4(6)	64(4)	3(4)	10(0)	-	-
4 Trichoptera (larvae)	4(10)	367(32)	3(5)	116(7)	15(20)	328(13)	-	-
5 Ephemeroptera (larvae)	1(2)	25(2)	-	-	12(16)	170(7)	-	-
6 Plecoptera (larvae)	2(5)	13(1)	-	-	8(11)	28(1)	-	-
7 Heteroptera (adults)	3(7)	37(3)	2(3)	28(2)	1(1)	15(1)	-	-
8 Heteroptera (larvae)	2(5)	14(1)	-	-	-	-	-	-
9 Vertebrata (eggs, larvae)	-	-	-	-	5(6)	192(8)	-	-
Subtotal	20(50)	653(58)	14(22)	236(14)	46(61)	748(30)	-	-
<i>Terrestrial</i>								
10 Isopoda	-	-	3(15)	68(4)	2(3)	16(1)	-	-
11 Myriapoda	2(5)	32(3)	6(9)	67(4)	-	-	2(17)	18(0)
12 Pseudoscorpionida	-	-	-	-	1(1)	0(0)	-	-
13 Araneida	4(10)	35(3)	7(10)	73(4)	4(5)	11(0)	2(17)	13(0)
14 Gastropoda Pulmonata	1(2)	87(8)	6(9)	550(33)	2(3)	515(21)	6(50)	2694(99)
15 Collembola	-	-	2(3)	3(0)	-	-	-	-
16 Diptera (adults)	1(2)	6(0)	5(8)	29(2)	1(1)	0(0)	-	-
17 Coleoptera (adults)	2(4)	9(1)	2(3)	24(1)	-	-	1(8)	1(0)
18 Hymenoptera Formicidae	2(5)	16(1)	3(5)	12(0)	-	-	-	-
19 Hymenoptera Formicidae excluded	1(2)	2(0)	-	-	-	-	-	-
20 Lepidoptera (larvae)	-	-	1(2)	14(0)	-	-	-	-
Subtotal	12(30)	186(16)	35(54)	840(51)	10(13)	542(22)	11(92)	2726(99)
<i>Land, shallow water or mud-dwelling</i>								
21 Acarina	-	-	-	-	1(1)	0(0)	-	-
22 Oligochaeta	2(5)	28(2)	6(9)	230(14)	4(5)	86(4)	-	-
23 Diptera (larvae)	1(2)	251(22)	8(12)	334(20)	8(11)	858(35)	1(8)	23(1)
24 Invertebrata unidentified	5(13)	22(2)	2(3)	14(0)	6(8)	9(0)	-	-
25 Vertebrata (<i>Discoglossus</i> froglets)	-	-	-	-	1(1)	203(8)	-	-
Subtotal	8(20)	301(26)	16(25)	578(35)	20(26)	1147(47)	1(8)	23(1)
Total	40	1140	65	1654	76	2437	12	2749
Standardized niche breadth <i>D_s</i>	0.544	0.300	0.769	0.299	0.523	0.356	-	-

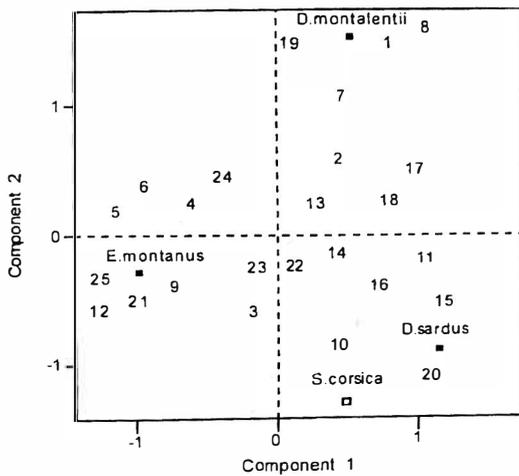


FIG. 1. Simple Correspondence Analysis plot showing the association between the diets of sympatric *D. montalentii*, *D. sardus*, *E. montanus* and their food categories (numbers correspond to prey categories in TABLE 2). *S. corsica* was added as a supplementary row element (see text).

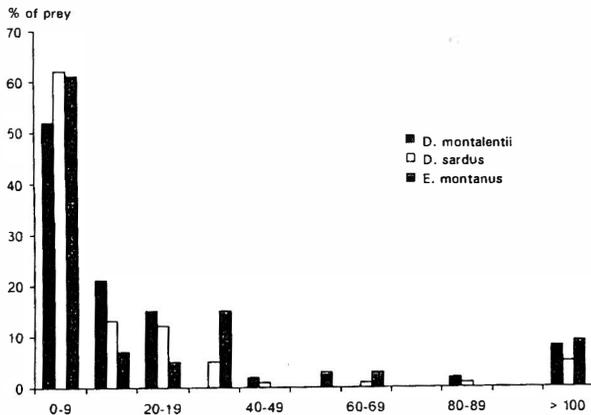


FIG. 2. Prey size distributions in sympatric *D. montalentii*, *D. sardus* and *E. montanus* from the Ospedale forest.

patterns of food utilization (Kolmogorov-Smirnov two sample test, $P > 0.10$ for all comparisons).

DISCUSSION

Discoglossus montalentii, *D. sardus*, and *E. montanus* were collected in or near aquatic habitats, where they were mating and spawning. At this time all three species should have been exposed to the same array of prey items. This may not be true, for example, in summer, when *E. montanus* adopts completely terrestrial habits (Goux, 1953; Michelot, 1992) and *D. montalentii* is still active in or near aquatic habitats (Salvidio *et al.*, unpublished data). The study species foraged on a wide variety of prey, suggesting a generalist foraging strategy. The presence in their diet of freshwater prey items indicated that they were all capable of swallowing their food under water. Thus, these findings confirm that *Discoglossus* are adapted to take prey underwater (Boulenger, 1897-1898) as newts do, a rather unusual behaviour in comparison to all other Eu-

ropean anurans (except for the discoglossid *Bombina*), which feed primarily on land, even during their aquatic breeding season (Chiminello & Generani, 1992; Nöllert & Nöllert, 1995). When prey size distributions were analysed, there were no statistically significant differences in prey utilisation between predators, despite their variation in body size (see Table 1). On the other hand, important taxonomic prey differences appeared when foraging behaviours were analysed. *Euproctus montanus* ingested mainly benthic hydrobionts, showing a clear tendency to feed in deep water. This foraging mode appeared qualitatively similar to that of the congener Pyrenean brook salamander *E. asper* (Montori, 1997). Conversely, *D. sardus* foraged mainly on land, while *D. montalentii* showed a mixed feeding strategy capturing prey both in terrestrial and aquatic microhabitats in similar proportions. These findings are most likely due to increased time spent foraging in different microhabitats by each species. Thus, these observations suggest more aquatic foraging behaviour for the Corsican painted frog, compared to the congeneric Tyrrhenian painted frog, at least during their reproductive period.

Prey type, and especially prey size, have been considered to play an important part in resource partitioning in amphibian assemblages (Toft, 1985). Differences in food size were usually related to the body size of the predator, while differences in prey type were attributable to habitat preferences, or to the time in which food is available (Pilorge, 1982). In the present case, amphibians were sampled in the same habitat, and thus the observed differences in food habits could be related to species-specific trophic behaviour. On the basis of these observations, these coexisting species seemed to partition food resources by adopting different foraging strategies, as contiguous microhabitats were exploited in different ways by the three species.

ACKNOWLEDGEMENTS

This study was undertaken as a part of research funded by the Ministère de l'Environnement Direction Régionale de l'Environnement de Corse (contract FN 237 53 95 000 14). Research permits (n° 96/263 and n° 97/342) were obtained from the Direction de la Nature et des Paysages. We thank B. Recorbet and M. Delaugerre for suggesting this research to us. G. Odierna performed chromosomal analysis on the discoglossid frogs; S. Kuzmin, and P. Joly provided useful comments on an early version of the manuscript.

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Accepted: 5.5.99