The diet of *Rana temporaria* Linnaeus, 1758 in relation to prey availability near its altitudinal limit

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Abstract

The diet of *Rana temporaria* (Linnaeus, 1758) was studied in the Gran Paradiso National Park, at and above the local timberline, up to the upper limit of its altitudinal distribution. A total of 128 adult frogs (length range: 3.7-9.0 cm) were captured from 2010 to 2012. Stomach content from 46 individuals was obtained by stomach flushing, of which 66% of the stomachs were empty. The diet composition was compared with the composition of the ground-dwelling invertebrate community, sampled by pitfall trapping. The number of prey items in the stomachs was lower at higher altitude and during the breeding season, when most of the stomachs were empty. *R. temporaria* feeds on a large number of taxa (in order of abundance: Coleoptera, Diptera, Hymenoptera, Opiliones, Araneae, Lepidoptera, Plecoptera, Trichoptera, Orthoptera, Acarina and Chilopoda), including a single observation of cannibalism on a freshly metamorphosed frog. There is a strong similarity between prey composition and availability. Therefore, near its altitudinal limit, *Rana temporaria* shows a generalist and slightly selective predatory behavior.

Key words: Gran Paradiso National Park, stomach flushing, cannibalism, pitfall traps, ground dwelling invertebrates.

INTRODUCTION

Rana temporaria Linnaeus, 1758 (Anura, Ranidae) has a large distribution range, including most of Europe as far north as northern Scandinavia and as far east as the Urals; within Europe, it is the only amphibious species that is able to colonize the northernmost and highest habitats (GASC ET AL., 1997). This is possibly due to its ability to survive through the winter, prolonging hibernation up to nine months per year (TATTERSALL & ULTSCH, 2008). This long hibernating period requires very large energy reserves, which are stored in the form of body fat and liver glycogen during a very short post-breeding activity period (PASANEN & KOSKELA, 1974, WELLS, 2010). Under such strong selective pressures, its feeding behavior could play a central role in allowing *R. temporaria* to survive at high latitudes and altitudes.

Various authors investigated the feeding habits of *R. temporaria* (KUZNETZOV, 1926, KRASSAVTZEV, 1935, BALCELLS, 1957, SAVAGE, 1961, GUYETANT, 1967, ASHBY, 1969, HAAPANEN, 1970, ITAMIES & KOSKELA, 1970, HOUSTON, 1973, BLACKITH & SPEIGHT, 1974, LOMAN, 1979, PILORGE, 1982, MORALES, 1984, PEDROCCHI & SANZ, 1984, VERSHININ, 1984, KUZMIN,

1990, KUZMIN & SUROVA, 1994, VIGNES 1995, RODRÍGUEZ ET AL., 1997, GOSÁ & VIGNES, 2000, DROBENKOV ET AL., 2005, STOJANOVA & MOLLOV, 2008, HODISAN ET AL., 2010, KOVÁCS ET AL., 2010). Most of these studies were carried out in comparatively warmer regions and, to the best of our knowledge, none in the Alps. The present study was carried out in the Gran Paradiso National Park (GPNP, Western Italian Alps), close to the highest reproductive site for *R. temporaria* (2799 m a.s.l., Gias de Beu lake; TIBERTI & VON HARDENBERG, 2012). The aim of the present study is to describe the diet of *R. temporaria* in the alpine environment, at the edge of its upper altitudinal distribution (VENCES ET AL., 2003). Some results were provisionally presented at the X Congress of the Societas Herpetologica Italica (ROLLA & TIBERTI, 2014).

MATERIALS AND METHODS

Study area

The GPNP is a large protected area in the Western Italian Alps (Figure 1), showing a large altitudinal extension (between 800 and 4061 m a.s.l.) and a typical alpine climate. All of the sampling areas for *R. temporaria* stomach contents (Figure1) and ground-dwelling invertebrates are included in the protected area. A short description of each sampling area is provided in Table 1.

Stomach contents

Frogs were opportunistically captured in nine sampling areas (Table 1; Figure 1), during a long-term monitoring campaign of aquatic environments in the Park. During the breeding season, only non-paired frogs were captured, to avoid disturbing mating. Stomachs were immediately flushed on the site, as described in SOLÉ ET AL. (2005), by using a 50 mL syringe filled with clear drinking water connected to a flexible PVC tube (diameter = 3 mm, length = 20 cm). Regurgitated items were stored in ethanol (70%). We mapped the sampling point and recorded the snout–vent length (SVL; accuracy ± 1 mm), the sex of each frog, and if the frog was collected during the breeding season or not. No frogs were injured, and all of the individuals were immediately released at the same sampling site after flushing, showing a normal escape behavior and unchanged health conditions. Samples were examined using a stereoscope and food items were usually recognized at the order level.

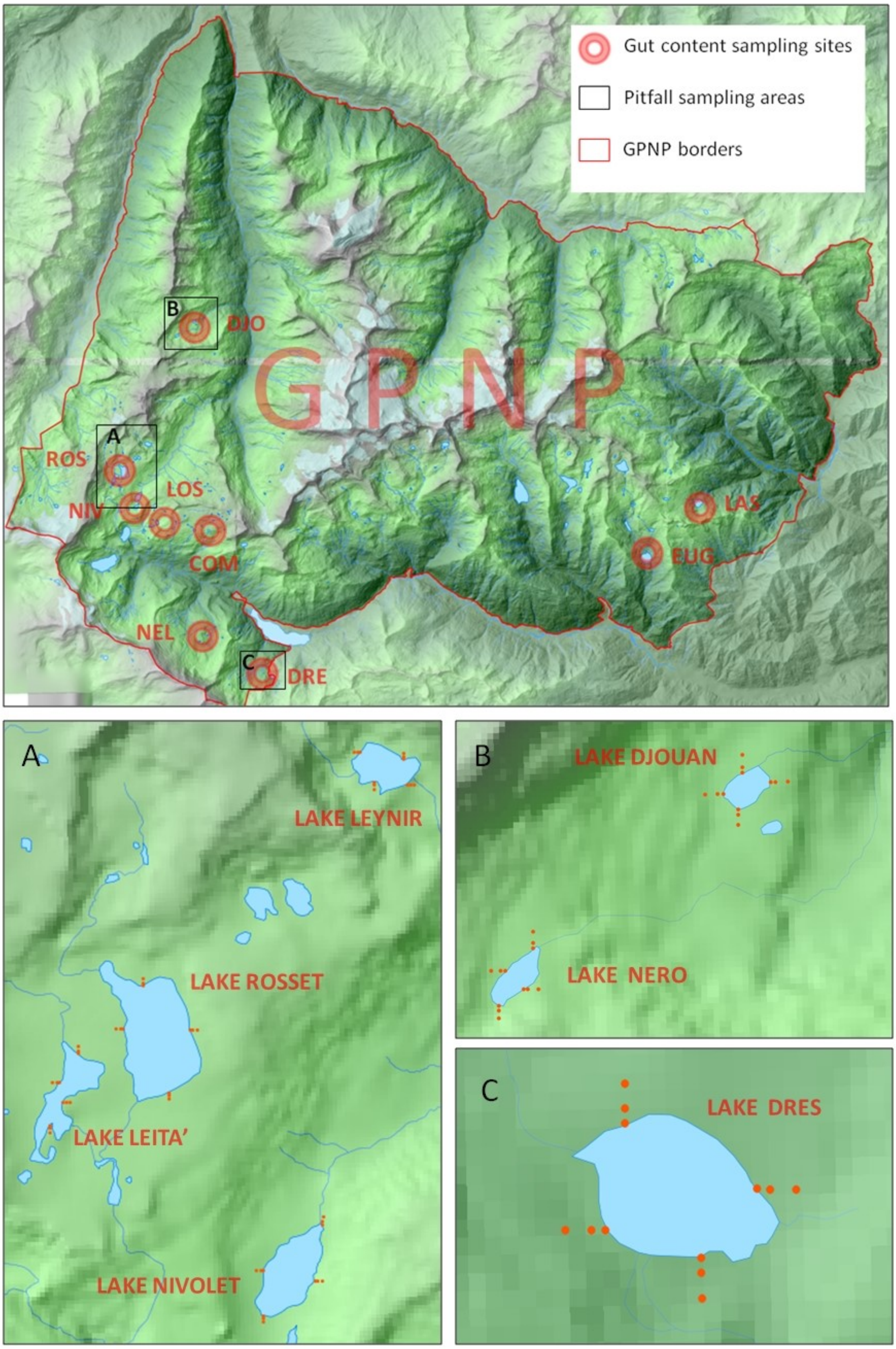

Figure 1. Sampling areas for the stomach contents of *Rana temporaria* (see Table 1 for the description) in the Gran Paradiso National Park, and pitfall traps' position (red dots in panels A-C) around seven high altitude lakes.

Table 1. Characteristics of the sampling sites of the *Rana temporaria* gut contents. The number of captured frogs and sampled gut contents at each site is reported. AG: acidic gneiss; CF: calcareous formations.

Sampling site	Altitudinal range (m a.s.l.)	Toponims and Habitats	Geology	N frogs	N gut contents
COM	2700-2800	Comba lakes: two lakes and several ponds surrounded by sparse vegetation and bare rocks.	AG	3	1
ROS	2700-2800	Rosset plains: some large lakes, several ponds and alpine streams surrounded by prairies.	CF	23	2
NIV	2500-2600	Nivolet plains: two alpine lakes and several ponds surrounded by prairies and bare rocks.	AG-CF	35	20
LOS	2500-2700	Losere lakes: three lakes and several ponds surrounded by sparse vegetation and bare rocks.	AG-CF	33	8
DJO	2500-2600	Djouan area: two lakes, ponds and peat bogs surrounded by alpine prairies.	CF	1	0
NEL	2000-2100	Nel plains: a large alpine peat bog.	AG	6	1
DRE	2000-2100	Dres area: an alpine lake, some ponds and some large peat bogs surrounded by prairies and bare rocks	AG	21	10
LAS	2000-2100	Lasin lake: one large alpine lake surrounded by prairies and bare rocks.	AG	1	0
EUG	1800-2000	Upper Eugio valley: one large alpine lake, small ponds and peat bogs surrounded by shrubland, prairies and bare rocks.	AG	5	4
		TOT		**128**	**46**

Prey availability

Pitfall traps (50 mm inner diameter, 70 mm deep, 1/3 filled with a 1:1 solution of water and vinegar) were used to sample ground-dwelling arthropods (Cole et al. 1992) around the lacustrine sampling sites (Figure 1) in August-September 2009. The traps were protected with flat stones and placed at 1, 10 and 50 meters from the coastline, along four transects placed at the four cardinal points (12 traps per lake). Pitfall traps were left in the field for 9-13 days. A total of 68 samples were obtained (16 traps were flooded or disturbed by cattle) all of which were preserved in 70% ethanol and sorted to class/order. Alpine lakes and the surrounding wetlands are commonly used by *R. temporaria* as breeding sites and feeding grounds. The winter ice cover in these aquatic habitats can persist up to nine months per year (TIBERTI ET AL., 2013). Most of the gut contents (67%) were collected in the areas where pitfall sampling for ground dwelling invertebrates was performed.

Data analysis

Statistical analyses were performed using R.3.1.1 (R DEVELOPMENT CORE TEAM, 2010). A multivariate linear regression was used to determine which factors influenced the number of food items found in the stomach contents. The log+1 transformed of the number of food items contained in each stomach was added to the model as a dependent variable; the altitude at which frogs were collected, SVL length, sex, and the season (binary variable: breeding vs. post breeding season) were added as covariates.

Sampling adequacy for diet composition was determined using Lehner's formula $Q = 1 - (N_1/I)$ (LEHNER, 1996), rising from 0 to 1, where Q is sampling adequacy, N_1 is the number of the food components occurring only once, and I is the total number of the food components.

RESULTS

A total of 128 adult *R. temporaria* (length range: 3.7-9.0 cm; 27 females, 88 males and 13 undetermined) were captured from 2010 to 2012 between 1860 and 2770 m a.s.l. (mean: 2474 m a.s.l.) at and above the local timberline. Most of the stomachs (64.1%) were empty and the mean number of contained food items was 1.0 (range from 0 to 11), or 2.8 considering only non-empty stomachs. The number of food items was higher during the post breeding season (79.1% of the stomachs flushed during the breeding season was empty) and decreased with altitude (Table 2).

The taxonomical composition of the prey in 46 non-empty stomachs is presented in Table 3 together with a prospect of the prey availability. The preyed taxa are -in order of abundance- Coleoptera, Diptera, Hymenoptera, Opiliones, Araneae, Lepidoptera, Plecoptera, Trichoptera, Orthoptera, Acarina and Chilopoda, and include a case of cannibalism on a freshly metamorphosed frog, one case of dermatophagy, and two cases of predation on aquatic taxa. In accordance with Lehner's index, the sampling adequacy was equal to 0.73.

DISCUSSION

Our results confirm that *R. temporaria* does not usually feed during the reproductive period (ITAMIES & KOSKELA, 1970, TATTERSALL & ULTSCH, 2008). When amphibians prolong the winter fasting and breed before beginning to feed, as in the case of *R. temporaria* (TATTERSALL & ULTSCH, 2008, WELLS, 2010), energy storage prior to overwintering should also account for the energy costs of reproductive activity, therefore becoming an even more challenging trial for *R. temporaria*. One could speculate that in extreme alpine habitats the feeding season is limited to a very short period and thus the feeding activity should be more intense than elsewhere. However, the number of food items in non-empty stomachs (2.8) was lower than what observed in different areas (e.g. 3.3-3.5 in KUZMIN, 1990; 3.9-7.4 in KUZMIN & SUROVA, 1994; 3.8 in STOJANOVA & MOLLOV, 2008; 10.7 in KOVÁCS ET AL., 2010; 14.7 in RODRUIGUEZ ET AL., 1997), and negatively influenced by altitude, possibly resulting from a lower prey availability at high altitudes, or from a different sampling season (e.g. many frogs from the present study were collected during the breeding season).

Table 2. Multivariate linear regression results summary: estimates β, degrees of freedom (df), associated F value and significance level *p* for all fixed terms in the analysis. Dependent variable: log+1 transformed number of prey items found in the stomachs of *Rana temporaria*. Model is based on 128 observations. **(Explanation in Croatian is missing)**

Model terms		β	df	F	*p*
Intercept		2.665	-	-	**<0.001**
Altitude		-0.001	1	5.94	**<0.05**
Season	breeding vs. post breeding	-0.397	1	14.87	**<0.001**
Sex	female vs. male	-0.145			
	female vs. undetermined	0.348	2	1.90	0.15
	undetermined vs. male	-0.493			
SVL length		-0.077	1	1.26	0.26

Table 3. Taxonomic composition of *Rana temporaria* diet (from 46 stomachs) and of the ground dwelling invertebrate community (from 139 pitfall traps), showing total numbers and percentages of different taxa that were found in the stomachs or in the traps. Insect larvae are given separately from their imagines as they are different prey categories as mobility and habitat use. “i”: imagines; “l”: larvae. **(Explanation in Croatian is missing)**

	Gut content			**Prey availability (pit fall sampling)**		
Taxon	**Total no. of food items**	**% of food items**	**% of stomachs**	**Total no. of potential prey**	**% of potential prey**	**% of traps**
ANELLIDAE						
Oligochaeta[1]	1	0.8	2.2	-	-	-
ARTHROPODA						
Chilopoda	1	0.8	2.2	5	0.2	6.4
Collembola	-	-	-	45	1.8	9.0
Acarina	1	0.8	2.2	396	16.2	32.1
Aranea	6	4.7	13.0	104	4.3	55.1
Opilionidae	7	5.5	15.2	105	4.3	46.2
Diptera, i	33	25.8	43.5	1447	59.1	84.6
Imenoptera, i	13	10.2	19.6	151	6.2	41.0
Coleoptera, i	38	29.7	52.2	70	2.9	59.0
Coleoptera, l	5	3.9	8.7	-	-	-
Eteroptera, i	-	-	-	101	4.1	16.7
Lepidoptera, l	8	6.3	13.0	10	0.4	9.0
Ortoptera	3	2.3	4.3	9	0.4	10.3
Plecoptera, i	2	1.6	4.3	-	-	-
Plecoptera[1], l	2	1.6	4.3	-	-	-
Tricoptera, i	6	4.7	4.3	-	-	-
CORDATA						
Rana temporaria[2]	2	1.6	4.3	4	0.2	5.1
TOT	**128**			**2447**		

[1] Aquatic taxon; [2] one frog skin and one fresh metamorphosed *Rana temporaria* found on the 16th August, 2012 in the stomach content of a 7.2 cm long male *R. temporaria* close to the shore of lake Losere (latitude N: 45°28’32”; longitude E: 07°09’25”; alt: 2568 m a.s.l.).

In addition sampling at different times could reveal different foraging activities, for example GOSÁ & VIGNES (2000) report that *R. temporaria* from the Iberian peninsula shows a feeding peak at midnight, while the frogs of the present study were usually collected in the central hours of the day and in any case during the daytime.

The sampling adequacy was 0.73, suggesting that a few potential prey taxa may be absent from our sampling. *R. temporaria* from our study area feed on a large number of prey taxa. We also found one case of cannibalism on a freshly metamorphosed frog, one case of dermatophagy, and the presence of a few aquatic preys (two stonefly larvae and an aquatic microdrile). Dermatophagy is common in congeneric species (e.g. *Rana dalmatina* and *Rana* synkl. *Esculenta*; GUIDALI ET AL., 2009) and in many other amphibians (WELDON ET AL., 1993). Cannibalism is common in *R. temporaria* tadpoles, sometimes feeding on dead adults and larval conspecifics, while it has been rarely reported between terrestrial life stages in natural conditions (see KUZMIN, 1991) or in captivity (BALCELLS, 1957). This observation could indicate that the stronger food limitation at higher altitudes could enhance cannibalistic behavior in adult *R. temporaria*. Cannibalism is also a quite common phenomenon in some congeneric species (e.g. *Rana ridibunda*; RUCHIN & RYZHOV, 2002).

Concerning the presence of aquatic taxa in the stomach contents, *R. temporaria* forage almost exclusively on land (e.g. KUZMIN, 1990) and underwater feeding is very rare or doubtful (some aquatic prey could become accessible when the puddles dry out, or incidentally drift into the mouth of the frog). However, this is not the first time that aquatic preys are found in the diet of *R. temporaria* (see SAVAGE, 1961, RODRÍGUEZ ET AL., 1997), and underwater feeding behavior cannot be excluded.

We observed a strong similarity between prey availability and diet composition, although Diptera were strongly dominant in the ground-dwelling invertebrate community, while they are just the second preferred food item for *R. temporaria*. This could be the result of the attractive effect of vinegar on some taxa (e.g. muscidae flies) generating a biased sample of ground-dwelling arthropods. The type of preservative is, indeed, a factor potentially affecting the selectivity and efficiency of pitfall traps (CHELI & CORLEY, 2010). However, apart some differences in the relative abundance between prey availability and consumption, all the available taxa were consumed by *R. temporaria*. The only exception is Collembola, a very small sized arthropod, which is probably below the minimum prey size for adults of *R. temporaria*. On the other hand, there are a few taxa preyed upon (e.g. Tricoptera and Plecoptera) that were not found in the pitfall traps, probably because they do not behave as ground-dwellers.

Compared to what was observed under less extreme climatic conditions, some taxa are absent in the diet of *R. temporaria* from high altitudes in the Alps, such as slugs and earthworms, which can be an important, if not dominant (SAVAGE, 1961), food resource at lower altitudes. For example, in other areas, terrestrial Gasteropoda accounts for up to the 25% of the diet of *R. temporaria* (DROBENKOV, 2005). Their absence in the diet is probably just the direct consequence of their absence from the available prey pool. When accounting for prey availability, our results are consistent with what is observed in other study areas, where *R. temporaria* usually feeds on the most abundant prey taxa. Due to this opportunistic feeding behavior, the diet of *R. temporaria* might be dominated by different taxa. For example, the most frequent prey can be either Plecoptera (Pyrenees; MORALES, 1984), Aracnida (Pyrenees and Massif Central; BALCELLS, 1957, PILORGE, 1982), Dermaptera (Pyrenees; PEDROCCHI & SANZ, 1984), Gasteropoda (SAVAGE, 1961) and Coleoptera (Poland and Romania; STOJANOVA & MOLLOV, 2008, KOVÁCS ET AL., 2010).

In conclusion, we did not observe any remarkable peculiarity in the diet composition of *R. temporaria* from high altitudes compared to what observed in other environments, and the main differences should be attributable to the prey availability rather than to an adaptation to the alpine climate. Furthermore, in our study area *R. temporaria* behaves as a generalist predator, probably consuming all mobile objects, large enough to be seen and small enough to be swallowed. The feeding adaptation to high altitudes should probably be studied with the timing of fat storage and consumption rather than in the quality and quantity of prey ingested (JÖNSSON ET AL., 2009). For example, it has been demonstrated that the maximum seasonal abundance of body fat coincides with the onset of hibernation only for *R. temporaria* from higher altitudes and latitudes, while the populations from warmer climates progressively lose their fat reserves during the autumn, before entering hibernation, despite the frogs remaining active and continuing to feed (PASANEN & KOSKELA, 1974, JÖNSSON ET AL., 2009).

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