Dietary overview of *Pelophylax perezi* from Monegros rice fields (northeast Spain)

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Amphibians are sensitive indicators of habitat degradation. Understanding their dietary patterns in altered landscapes is fundamental to understanding the effects of habitat loss worldwide. A stomach content analysis was conducted on *Pelophylax perezi*, an endemic anuran heavily colonizing rice fields in Monegros, an arid region in northeast Spain. The taxonomic range of prey consumed by this species was compared with prey availability and dietary changes were evaluated among frog size groups. Small adult insects (dipterans, coleopterans, ants and heteropterans) were the main diet, indicating an active foraging mode. Frogs showed no preference for any prey taxa. Larger frogs consumed a higher volume of food, but relatively fewer prey than smaller individuals. A large niche breadth was recorded for all groups. Food partitioning was lowest between distant size groups. Maximum prey size was significantly related to morphological constraints such as frog size and mouth width. Bigger frogs preyed on larger items while also foraging on smaller ones, indicating no prey size selection. Overall, *P. perezi* had a generalist feeding pattern dictated mainly by prey availability. These food habits may help the species to persist in the agricultural landscape of this arid region.

Key words: diet, electivity, niche breadth, prey size selection, rice paddies, Monegros arid region

INTRODUCTION

One of the major threats to amphibian populations worldwide is agricultural land use, causing habitat degradation and loss and contributing to the decline of many species (Green, 1997; Collins & Crump, 2009). Owing to their biphasic life, anurans are important components of food-webs in both aquatic and terrestrial environments. The expansion of land cultivation and associated habitat modifications such as increased mechanization, irrigation and agrochemical use have influenced anuran feeding ecology by decreasing the number of foraging habitats (Joly et al., 2001). Studies on fundamental aspects of their life history in impacted habitats are therefore becoming increasingly important.

Amphibians are usually regarded as generalist predators, categorized as either active foragers or sedentary "sit-and-wait" predators (Duellman & Trueb, 1986). Their dietary patterns are regulated by extrinsic factors such as prey availability, presence of competitors and predation risks, and by intrinsic factors such as morphological constraints resulting from ontogeny, body size and specialization (Hirai & Matsui, 1999). Body size can affect foraging in several ways, including size/age-related foraging ability and prey choice (Duellman & Trueb, 1986); in small frogs, gape size limits their range of prey relative to the food available in the habitat (Newman, 1999).

Pelophylax perezi is an anuran endemic to the Iberian Peninsula and southern France. The species is vulnerable to land use change and agricultural management (Pastor et al., 2004), which have resulted in population declines in some areas (Crochet et al., 2004). Yet in Monegros, an arid region of northeast Spain, *P. perezi* became the most common amphibian in areas irrigated in the 1960s (Pedrocchi, 1998). However, very little is known about anuran diets, a key factor that affects all aspects of species life histories, in these areas. Previous studies of *P. perezi*'s feeding habits have reported a generalist diet, based primarily on small (3–6 mm) dipterans, coleopterans and hymenopterans (Hódar et al., 1990; Lizana et al., 1986; Jover, 1989). The aim of the present study was to determine the taxonomic range of prey consumed by *P. perezi*, and to evaluate qualitative and quantitative changes in the diet among frog size groups inhabiting rice fields in Monegros. As rice cultivation generally yields a high abundance of arthropods, we hypothesized that prey size and number would be correlated with body size. We predicted that larger individuals would eat a wider variety of prey items, and that they eat more and larger prey than smaller frogs. The information collected could help in analysing ranid community structure on the basis of food utilization in rice fields in arid regions.

STUDY AREA AND METHODOLOGY

Area description

Monegros (northeast Spain) is one of the most arid regions in Europe (Herrero & Snyder, 1997). It lies in the central part of the Ebro river basin, surrounded by the Pyrenees in the north, the Iberian mountain chain in the southwest and the Catalonian coastal ranges in the southeast. The long-term average annual temperature is 14.5 ºC, with extremes from –15º C to above 43 ºC. The mean annual rainfall is low (360 mm), concentrated mainly in spring and autumn and characterized by high inter-annual variability (Comín & Williams, 1993).

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During the last three decades, Monegros has been increasingly used for intensive agriculture, with rice being one of the main crops. The region has been identified as being particularly vulnerable to human and climate-induced land degradation (Macklin et al., 1994).

Sampling of *P. perezi* and stomach content analysis

A total of 151 individuals of *P. perezi* between 21 and 86 mm in length were captured with a hand net during 12 censuses between 4 July and 26 September 2003 (after the reproductive season) in five rice-growing areas in San Juan del Flumen, central Monegros (41°46.4′N; 00°12.8′W; 300 m a.s.l.), about 2 km apart. Immediately after capture the individuals were stomach flushed at least three times until no additional items were obtained (following Legler & Sullivan, 1979). The volume of stomach contents was estimated to the nearest 0.1 ml by measuring the volume of water displaced by the total food contents in a graduated cylinder. The stomach contents were then preserved in 70% ethyl alcohol. Ten frogs had empty stomachs and were excluded from further analysis. For each frog we recorded snout–vent length (SVL) and mouth width to the nearest 0.5 mm, and body mass to the nearest 0.1 g. Individuals were toe-clipped to avoid recapturing and released at their sites of collection. In the laboratory, prey items were identified to the lowest possible taxonomic level allowed by their state of digestion. Next, the prey were counted and their total length measured to the nearest 0.1 mm with electronic callipers.

In order to estimate prey availability we deposited 10 yellow pan traps (25 cm diameter/1 cm depth) spaced 25 m apart on the rice paddy borders of the five capture areas. This method uses dishes filled with soapy water that serve as both attractant and pitfall traps (Le Berre & Roth, 1969). Sampling was conducted two days per month (24 hours each), simultaneously with frog collection. We assumed that the technique provided a good approximation of prey availability, because it reliably collected beetles and ants, which are important food items for *P. perezi* (Hódar et al., 1990). Additionally, 1 m² net sweeps (1 mm mesh size) were conducted to assess the availability of aquatic prey.

Data processing

Frogs were divided into four size groups: 1) ≥31 mm (*n*=37), 2) 32–34 mm (*n*=38), 3) 35–39 mm (*n*=28) and 4) ≥40mm (*n*=38). The first group is represented by young postmetamorphs, followed by juveniles (groups 2 and 3), while the fourth group were considered adults. Data analysis included qualitative (diet composition, electivity, niche breadth and overlap) and quantitative (diet optimization and prey–frog morphologic relationships) evaluations.

The main prey items (ants, dipterans and coleopterans) of *P. perezi* were compared along a latitudinal gradient by using percentage coefficient of variation (%CV) and Pearson product-moment correlation coefficients (*r*). The correlations, together with 95% confidence intervals (CI), were estimated after 997 bootstrap resamplings. This procedure involves repeating the correlation on different

samples randomly drawn from the original dataset to construct a 95% CI. This should reduce bias in the analysis due to seasonal or habitat influences.

In order to determine the degree of relationship between prey availability and diet composition, we calculated Ivlev's electivity index (Ivlev, 1961): $E = (r_i - p_i)/(r_i + p_i)$, where r is the proportion of the ith prey item in the diet, and p is its proportion in the environment. This index scales symmetrically from –1 (avoidance) to 1 (preference), with 0 representing non-selection.

Dietary niche breadth of each frog group helped to determine dietary changes along development; we used Smith niche breadth index (Smith, 1982) with 95% confidence intervals:

$$NB = \sum_{i=1}^{n} (p_i q_i)^{(1/2)}$$

where p_i is the proportion of resource i used, q_i is the proportion of resource i available, and n is the number of prey categories. *NB* values vary between 0 and 1; the higher the value, the broader the niche, and the less selective the consumer.

The degree of similarity in prey use between frog groups was determined by the niche overlap index (Lawlor, 1980):

$$O = \sum_{i=1}^{n} a_{ij} a_{kj} \bigg/ \sqrt{\sum_{i=1}^{n} a_{ij}^{2} \sum_{i=1}^{n} a_{kj}^{2}}$$

where a_{ij} refers to the proportion of resource j used by individual i divided by the proportion of resource j available; a_{kj} is defined similarly for a second frog size group. The index values range from 0 to 1, with 1 indicating identical resource use. Values of niche overlap are presented as percentages.

Prey number and volume of stomach contents were compared between frog groups by Kruskal–Wallis nonparametric ANOVA. Additionally, we examined the relationships between frog morphometric characteristics (body size, mass and mouth width) by quadratic regres-
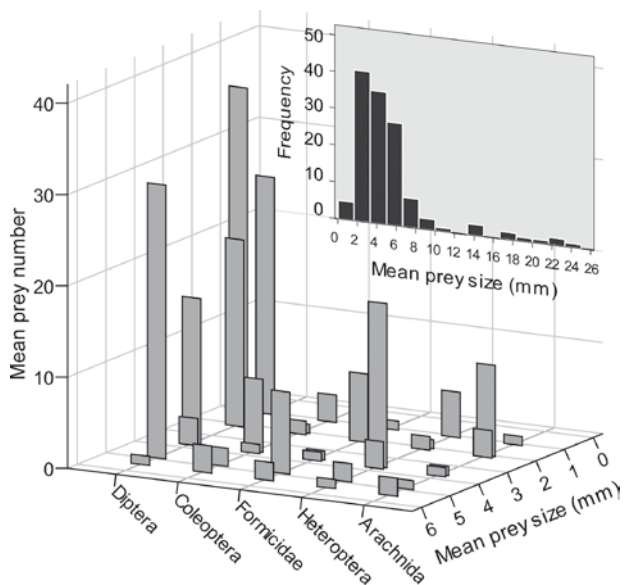
Fig. 1. Mean prey number and size of the main food taxa in the diet of *Pelophylax perezi*. Inset is a frequency distribution of mean prey size.

Table 1. Diet spectrum of *Pelophylax perezi* (*n*=141) in Monegros rice fields, based on stomach content analysis. *n* = number of items; *n*(%) = numeric proportion of different prey items; F = frequency of occurrence, defined as the number of frogs preying on a particular type of food; F(%) = percentage of occurrence.

Prey taxon	*n*	*n* (%)	F	F (%)
Class Insecta				
Diptera				
Subord. Nematocera (others)	1521	60.50	117	82.98
Fam. Chironomidae	6	0.24	2	1.42
Fam. Ceratopogonidae	2	0.08	2	1.42
Subord. Brachicera	262	10.42	71	50.35
Fam. Tabanidae	1	0.04	1	0.71
Coleoptera				
Fam. Hydrophilidae	87	3.46	47	33.33
Fam. Dytiscidae	85	3.38	48	34.04
Fam. Hydraenidae	13	0.52	10	7.09
Fam. Anthicidae	11	0.44	5	3.55
Fam. Staphylinidae	9	0.36	8	5.67
Fam. Carabidae	8	0.32	5	3.55
Fam. Scolytidae	4	0.16	3	2.13
Fam. Curculionidae	2	0.08	2	1.42
Fam. Coccinelidae	1	0.04	1	0.71
Fam. Hysteridae	1	0.04	1	0.71
Fam. Scarabeidae	1	0.04	1	0.71
Fam. Ostomidae	1	0.04	1	0.71
Fam. Chrysomelidae	1	0.04	1	0.71
others	21	0.84	19	13.48
Dermaptera				
Fam. Forficulidae	3	0.12	3	3.55
Hymenoptera				
Subord. Apocrita (others)	4	0.16	4	2.84
Fam. Formicidae	183	7.28	54	38.30
Subord. Symphyta	6	0.24	3	2.13
Heteroptera				
Fam. Gerridae	54	2.15	29	20.57
Fam. Pleidae	41	1.63	22	15.6
Fam. Corixidae	30	1.19	18	12.77
Fam. Veliidae	26	1.03	15	10.64
Fam. Mesoveliidae	15	0.60	8	5.67
Subord. Geocorisae	11	0.44	10	7.09
Subord. Hydrocorisae	3	0.12	3	4.96
Fam. Acanthosomatidae	2	0.08	2	1.42
Fam. Aphelocheiridae	1	0.04	1	0.71
Fam. Notonectidae	1	0.04	1	0.71
others	3	0.12	3	4.96
Homoptera				
Fam. Aphidae	5	0.20	5	3.55
Lepidoptera	2	0.08	2	2.13
Odonata				
Subord. Zygoptera	4	0.16	3	2.13
Colembola	1	0.04	1	0.71
Thysanoptera	1	0.04	1	0.71
Mallophaga	2	0.08	2	1.42
Class Arachnida				
Araneae				
others	28	1.11	28	21.99
Fam. Opilionidae	2	0.08	2	1.42
Subord. Hydracarina	17	0.68	6	4.26
Class Ostracoda	7	0.28	4	2.84
Class Gastropoda				
Fam. Planorbiidae	19	0.76	19	14.18
Fam. Limneidae	6	0.24	4	2.84
TOTAL	2514		141	

sions and between frog morphology and prey size by linear regressions and Pearson correlations. Only frogs with at least two prey items in their stomachs (allowing maximum and minimum size estimations) were included in this analysis. Furthermore, stomach content volume was correlated with frog size and body mass. All analyses were performed in Statistica and SPSS packages for Windows.

RESULTS

Altogether 2514 prey items (mean = 17.83±14.75 SD items per stomach) assigned to 45 taxa were identified in 141 stomachs of *P. perezi*. In general, the stomachs contained a large number of small preys (Fig. 1). Adult insects made a substantial contribution to the diet (96.56%), with the remaining 3.44% being represented by other small arthropods (e.g. spiders and ostracods) and molluscs (snails). Insect larvae and pupae represented only 7.32% and 0.91% of all prey items, respectively. The dominant type was terrestrial, including ground-dwelling and aerial prey items (71.36%), followed by aquatic prey (28.64%). Dipterans recorded the highest numerical dominance and frequency of occurrence, followed by coleopterans, hymenopterans (mainly ants) and heteropterans (Table 1). The amount of dipterans in our study appeared to reach a higher proportion when compared to other *P. perezi* populations, and also showed a high variation between locations (%CV = 71.17; Table 2). The proportion of ants tended to decrease with increasing latitude (r= –0.83, P=0.04, 95% CI = –1.00 to –0.22; Table 2). Beetles accounted for a rather low proportion when compared to other studies covering the same period (%CV = 85.83; Table 2).

To investigate prey choice, a total of 4296 potential prey items belonging to 11 taxa were sampled from the environment and compared with the recorded diet (Fig. 2). The electivity index shows that frogs had no apparent preference for any taxon (E<0.5, Fig. 2). Heteropterans, dipterans and coleopterans were the most eaten of the available prey (E=0.38, E=0.37, E=0.31, respectively; Fig. 2 and Table 1). Very small items such as springtails and aphids were generally avoided (E values close to –1; Fig. 2).

Pelophylax perezi had a relatively broad diet with similar niche breadth values at different post-larval stages: group 1, *NB*=0.71 (0.47–0.88 confidence interval); group 2, *NB*=0.79 (0.58–0.93); group 3, *NB*=0.75 (0.52–0.91); group 4, *NB*=0.75 (0.52–0.91). A relatively high niche overlap was recorded between size groups 1 and 2 (88.82%), followed by groups 2 and 3 (88.29%), 1 and 3 (85.77%), 2 and 4 (75.12%), and 3 and 4 (71.62%); the lowest overlap was between groups 1 and 4 (58.27%). Significant differences in stomach content volume and ingested prey numbers were observed between frog size classes (Kruskal–Wallis test, χ^2=20.61, df=3, P<0.01 and χ^2=28.28, df=3, P<0.01, respectively). Larger individuals ate fewer prey but had significantly larger stomach content volumes than smaller ones (Fig. 3). Dipterans recorded a significant decrease in number towards adult stages (Kruskal–Wallis test, χ^2=15.65, df=3, P=0.001).

Table 2. Variation in the proportions of ants and other dominant prey of *Pelophylax perezi* diet along a latitudinal gradient. Habitats: + = natural (rivers, wetlands); ++ = artificial (rice paddies, permanent artificial ponds). * = number of frogs sampled over the entire study period (February–December).

Study area	Latitude	No. frogs	Period	Formicidae (%)	Diptera (%)	Coleoptera (%)	Reference
Bizkaia[+]	43ºN	65	autumn	1.03	40.18	3.09	Docampo & Vega, 1990
Monegros[++]	41ºN	141	July–Sept.	7.28	71.28	9.76	This study
Girona	41ºN	–	–	–	6.74	49.16	Bea et al., 1994
Salamanca[+]	40ºN	199*	July–Sept.	14.00	31.00	18.32	Lizana et al., 1986
Aveiro[++]	40ºN	70	Feb.–Apr.	28.50	~ 9.20	7.50	Anastácio & Ferrand d'Almeida, 1995
Alicante	38ºN	–	one year	17.40	–	–	Hernández & Seva, 1985
Granada[+]	37ºN	135	Mar.–Oct.	37.78	45.93	54.07	Hódar et al., 1990

Mouth width and body mass increased with SVL ($r^2=0.96$, $P<0.01$; $r^2=0.99$, $P<0.01$; quadratic relationships). Body size, mouth width and body mass showed significant correlations with mean prey size ($r=0.49$, $P<0.01$; $r=0.42$, $P<0.01$ and $r=0.39$, $P<0.01$, respectively) and maximum prey size (Fig. 4). Minimum prey size was weakly associated with SVL and mouth width, but not with frog mass. Moreover, large frogs reduced their intake of very small prey (Fig. 4). The total prey volume was positively associated with SVL, body mass and mouth width ($r=0.33$, $P<0.01$; $r=0.31$, $P<0.01$ and $r=0.29$, $P<0.01$).

DISCUSSION

The high intake of adult insects such as flies and midges suggests an active-search foraging strategy (Berazategui et al., 2007). A comparison of the importance of dipterans, beetles and ants with literature data showed a large amount of variability between populations/regions (Table 2). The proportion of dipterans in the diet appeared to be high compared to other *P. perezi* populations (Table 2), which is probably a reflection of the abundance of this prey in the environment. Ants showed a tendency to decrease with increasing latitude (Table 2), consistent with Hernández & Seva (1985), who reported similar findings for members of the genus *Rana*. The number of ant species generally decreases significantly with increasing

Fig. 2. Ivlev's electivity index values for the main prey groups in the diet of *Pelophylax perezi*.

latitude along with an increase in body size (Cushman et al., 1993), and the diet of *P. perezi* might reflect ant abundance even across relatively short latitudinal gradients. Given the lack of information on prey availability in other studies it is impossible to fully establish that there is a latitudinal gradient effect on diet. However, our findings merit further exploration of this relationship, and it remains to be studied whether these differences in food intake are a function of habitat type, season or body size.

Terrestrial prey (aerial and ground-dwelling) represented the largest fraction in the frogs' diet, indicating that terrestrial habitats adjoining the rice paddies are very important in providing food resources. Less aggressive agricultural alteration of the paddies' surroundings, e.g. avoiding the use of herbicides for weed control, is therefore recommended for *P. perezi* populations inhabiting agricultural land, especially in sensitive regions such as Monegros.

The electivity index showed that *P. perezi* is an indiscriminate forager with regard to prey type (Fig. 2). This was also supported by the high niche breadth. An accepted view is that a relatively large dietary breadth provides high ecological resilience (Williams et al., 2006), as local frog populations can expand beyond their natural niche ranges (Hirai & Matsui, 2000). This behaviour is an effective strategy for a colonizer (Saenz, 1996) and may explain the ability of *P. perezi* to disperse to newly created habitats. The dietary changes between different life stages suggest that food partitioning plays an important role in frog community structure. This is also supported by previous studies that reported a spatial segregation between juvenile and adult *P. perezi* inhabiting temporary ponds in semiarid regions (Lizana et al., 1989).

Significant quantitative changes in diet occurred along the frog's developmental stages, as shown by increased volume of the stomach contents but lower prey numbers towards the adult stage (Fig. 3). Small individuals preyed on a large number of small items such as dipterans, which would facilitate rapid growth at this early stage. Given their small dimensions and generally active locomotion, dipterans may be energetically expensive to catch. However, it appears that small frogs preyed continuously on them throughout their active period in order to maintain a positive energy budget.
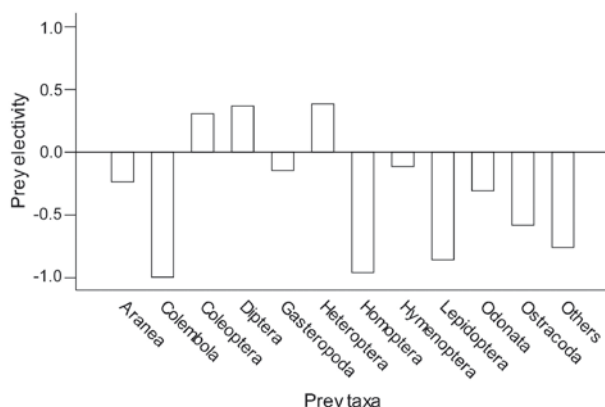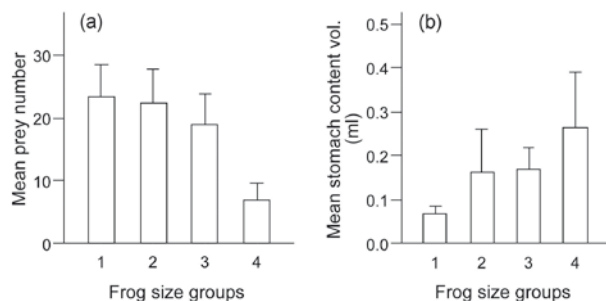
Fig. 3. Variations in (a) mean prey number and (b) average volume of stomach content between frog size groups. Figures represent mean values with 95% CI.

Larger frogs tended to eat larger prey while still ingesting smaller items (Fig. 4). This is in line with a theoretical model of diet efficiency proposed for predator–prey size relationships (Costa et al., 2008), in which larger predators target a wide prey size spectrum to maximize energy gains. This implies that the overall prey diversity would increase with size. However, the ingestion of small prey by adult frogs appears not to have an important impact on their dietary breadth. While the frogs did not exclude small items from their diet as they grew, it seems that their morphological limitations influenced maximum and mean prey size intake (Fig.4). This relationship could also explain the weak but significant increase in stomach content volume with size and mass. Furthermore, optimal foraging theory assumes that individuals act to maximize the rate of energy intake in accordance with morphological constraints (e.g. mouth width) and foraging ability (Schoener, 1971). Foraging on a broad prey size range while increasing maximum prey size may therefore result in higher energy reserves and, consequently, higher survival rates during extended periods of drought. Our findings are similar to results reported for northern *P. perezi* populations (Docampo & Vega, 1990) but different from eastern and western ones (Jover, 1989; Anastácio & Ferrand d'Almeida, 1995).

This study shows that *P. perezi* from the Monegros rice fields is a generalist feeder that uses the food resources available in the habitat as an opportunist predator. This widespread conserved feeding habit among ranids might account for the species' success in this altered landscape. Integrating adequate land management practices with knowledge of agro-ecosystem functioning would not only allow farmers to preserve the habitat of resident amphibians, but would also benefit rice field biodiversity, enhancing agro-ecosystem services.

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REFERENCES

Anastácio, P.M. & Ferrand d'Almeida, F. (1995). Food habits of *Rana perezi. Ciência Biologica Ecology and Systematics* 15, 21–31.

Bea, A., Montori, A. & Pascual, X. (1994). Herpetofauna dels Aiguamols de l'Empordà. In *Els Sistemes Naturals dels Aiguamols de l'Empordà*, 359–407. Gosálbez Noguera, J., Serra Raventós, J. & Velasco Batlle, E. (coord.). *Treballs de l'Institució Catalana d'Història Natural* 13.

Berazategui, M., Camargo, A. & Maneyro, R. (2007). Environmental and seasonal variation in the diet of *Elachistocleis bicolor* (Guérin-Méneville 1838) (Anura: Microhylidae) from northern Uruguay. *Zoological Science* 24, 225–231.

Le Berre, J.R. & Roth, M. (1969). Les méthodes de piégeage des invertébrés. In *Problèmes d'Ecologie: l'Echantillonnage des Peuplements Animaux des Milieux Terrestres*, 55–96. Lamotte, M. & Bourlière, F. (eds). Paris: Masson & Cie.

Collins, J.P. & Crump, M.L. (2009). *Extinction in Our Times: Global Amphibian Decline*. New York: Oxford University Press.
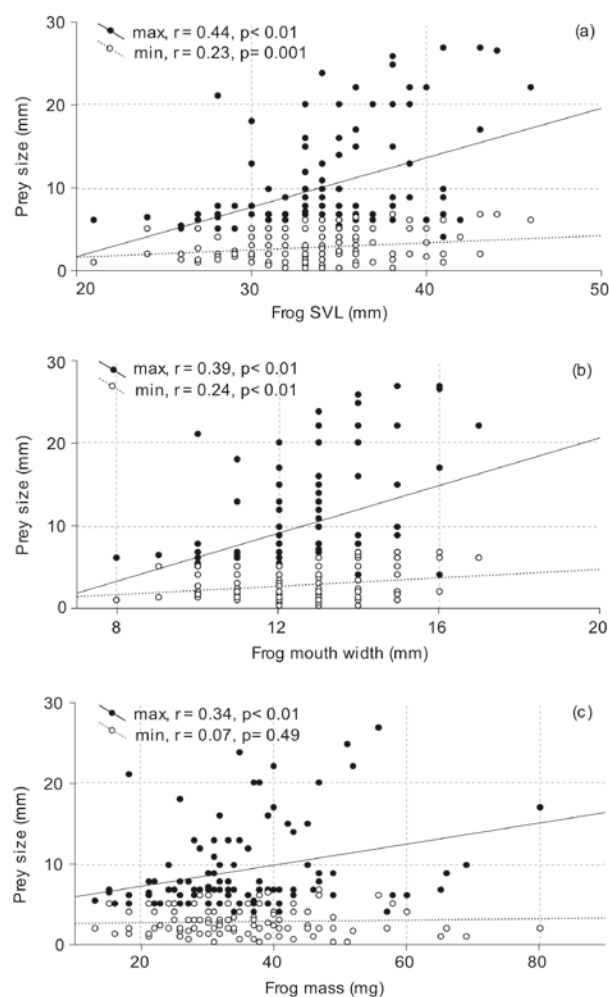
Fig. 4. Linear regressions of maximum and minimum prey size against: (a) frog size, (b) mouth width and (c) frog mass, with the corresponding fit lines, Pearson product correlation coefficients and *P* values.

Comín, F.A. & Williams, W.D. (1993). Parched continents: our common future? A paradigm of planetary problems. In *Limnology Now: A Paradigm of Planetary Problems*, 473–527. Margalef, R. (ed.). Amsterdam: Elsevier.

Costa, G.C., Vitt, L.J., Pianka, E.R., Mesquita, D.O. & Colli, G.R. (2008). Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17, 670–677.

Crochet, P.A., Chaline, O., Cheylan, M. & Guillaume, C.P. (2004). No evidence of general decline in an amphibian community of southern France. *Biological Conservation* 119, 297–304.

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993). Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95, 30–37.

Docampo, L. & Vega, M.M. (1990). Contribución al estudio de la alimentación de *Barbus bocagei* (Steindachner 1866), *Phoxinus phoxinus* (Linnaeus 1758) y *Rana perezi* (Seoane 1885) en los ríos de Bizkaia. *Scientia Gerundensis* 16, 61–73.

Duellman, W.E. & Trueb, L. (1986). *Biology of Amphibians*. New York: McGraw-Hill.

Green, D.M. (1997). Perspectives on amphibian population declines: defining the problem and searching for answers. In *Amphibians in Decline. Canadian Studies of a Global Problem*, 291–308. Green, D.M. (ed.). *Herpetological Conservation* 1. St Louis, MO: SSAR.

Hernández, A. & Seva, E. (1985). Datos preliminares sobre la alimentación de la rana común (*Rana perezi*) en la provincia de Alicante. *Ayudas a la Investigación* 3, 37–46.

Herrero, J. & Snyder, R.L. (1997). Aridity and irrigation in Aragón, Spain. *Journal of Arid Environments* 35, 55–547.

Hirai, T. & Matsui, M. (1999). Feeding habits of the pond frog, *Rana nigromaculata*, inhabiting rice fields in Kyoto, Japan. *Copeia* 1999, 940–947.

Hirai, T. & Matsui, M. (2000). Feeding habits of the Japanese tree frog, *Hyla japonica*, in the reproductive season. *Zoological Science* 17, 977–982.

Hódar, J.A., Ruiz, I. & Camacho, I. (1990). La alimentación de la rana común (*Rana perezi* Seoane, 1885) en el sureste de la Península Ibérica. *Miscellánia Zoologica* 14, 145–153.

Ivlev, V.S. (1961). *Experimental Ecology of the Feeding of Fishes*. Connecticut: Yale University Press.

Joly, P., Miaud, C., Lehmann, A. & Grolet, O. (2001). Habitat matrix effects on pond occupancy in newts. *Conservation Biology* 15, 239–248.

Jover, L. (1989). *Nuevas Aportaciones a la Tipificación Trófica Poblacional: El Caso de* Rana perezi *en el Delta del Ebro*. PhD thesis. Barcelona: University of Barcelona.

Lawlor, L.R. (1980). Overlap, similarity and competition coefficients. *Ecology* 61, 245–251.

Legler, J.M. & Sullivan, L.J. (1979). The application of stomach-flushing to lizards and anurans. *Herpetologica* 35, 107–110.

Lizana, M., Ciudad, P.M.J. & Pérez, M.V. (1986). Uso de los recursos tróficos en una comunidad ibérica de 240 anfibios. *Revista Española de Herpetología* 1, 207–271.

Lizana, M., Ciudad, P.M.J. & Pérez, M.V. (1989). Actividad, reproducción y uso del espacio en una comunidad de anfibios. *Treballs de la Societat Catalana d'Ictiologia i Herpetología* 2, 92–127.

Macklin, M.G., Passmore, D.G., Stevenson, A.C., Davis, B.A. & Benavente, J.A. (1994). Response of rivers and lakes to Holocene environmental change in the Alcaniz region, Teruel, north-east Spain. In *Environmental Change in Drylands*, 113–130. Millington, A. & Pye, K. (eds). Chichester: Wiley.

Martín, J., Luque-Larena, J.J. & López, P. (2005). Factors affecting escape behavior of Iberian green frogs (*Rana perezi*). *Canadian Journal of Zoology* 83, 1189–1194.

Newman, R.A. (1999). Body size and diet of recently metamorphosed spadefoot toads (*Scaphiopus couchii*). *Herpetologica* 55, 507–515.

Pastor, D., Sanpera, C., Gonzalez-Solís, J., Ruiz, X. & Albaiges, J. (2004). Factors affecting the organochlorine pollutant load in biota of a rice field ecosystem (Ebro Delta, NE Spain). *Chemosphere* 55, 567–576.

Pedrocchi Renault, C. (ed.) (1998). *Ecología de los Monegros*. Huesca: Instituto de Estudios Altoaragoneses y Centro de Desarrollo de Monegros.

Saenz, D. (1996). Dietary overview of *Hemidactylus turcicus* with possible implications of food partitioning. *Journal of Herpetology* 30, 461–466.

Schoener, T.W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2, 369–404.

Smith, E.P. (1982). Niche breadth, resource availability, and inference. *Ecology* 63, 1657–1681.

Williams, Y.M., Williams, S.E., Alford, R.A., Waycott, M. & Johnson, C.N. (2006). Niche breadth and geographical range: ecological compensation for geographical rarity in rainforest frogs. *Biological Letters* 2, 532–535.