

Disentangling the effects of predator body size and prey density on prey consumption in a lizard

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Summary

1. Understanding proximate determinants of predation rates is a central question in ecology. Studies often use functional response (density dependent) or allometric (mass dependent) models but approaches that consider multiple factors are critical to capture the complexity in predator–prey interactions. We present a novel comprehensive approach to understand predation rates based on field data obtained from a vertebrate predator.
2. Estimates of food consumption and prey abundance were obtained from 21 semi-natural populations of the lizard *Zootoca vivipara*. We identified the most parsimonious feeding rate function exploring allometric, simple functional response and allometric functional response models. Each group included effects of sex and weather conditions.
3. Allometric models reveal the importance of predator mass and sex: larger females have the highest natural feeding rates. Functional response models show that the effect of prey density is best represented by a Holling type II response model with a mass, sex and weather dependent attack rate and a constant handling time. However, the best functional response model only received moderate support compared to simpler allometric models based only on predator mass and sex.
4. Despite this limited effect of prey densities on feeding rates, we detected a significant negative relationship between an index of preferred prey biomass and lizard density.
5. Functional response models that ignore individual variation are likely to misrepresent trophic interactions. However, simpler models based on individual traits may be best supported by some data than complex allometric functional responses. These results illustrate the importance of considering individual, population and environmental effects while also exploring simple models.

Key-words: field experiment, functional response, Lacertidae, parsimony, prey–predator interaction, size-effect

Introduction

The study of prey–predator interactions and foraging behaviour can provide critical insights into the structure of food webs, population dynamics and species interactions (e.g. Persson *et al.* 1998; Abrams 2000; de Roos, Persson & Mccauley 2003; Gilg, Hanski & Sittler 2003; Miller *et al.* 2006). The foraging ability of a predator determines its

energy acquisition and ability to grow, survive and reproduce, but can also influence the fitness of conspecifics as predators may aid or interfere with each other (Arditi & Akcakaya 1990). Predation also has a large effect on prey populations influencing their dynamics, behaviour and spatial distribution (Reeve 1997; Gilg, Hanski & Sittler 2003). Predation rates are determined by several factors including prey and predator densities, body size, habitat structure and weather conditions (e.g. Avery 1971; Angilletta 2001; Pitt & Ritchie 2002; Miller *et al.* 2006). The field of foraging ecology has emphasized density-dependent effects defining functional responses that estimate prey consumption by an average predator as a function of prey, and in some cases

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predator, density (Holling 1959; Hassell & Varley 1969). However, these generalized functions fail to represent natural variation among individuals. Body size usually varies significantly among individuals with important consequences for the dynamics of prey–predator systems (Persson *et al.* 1998; Claessen, de Roos & Persson 2000; de Roos, Persson & McCauley 2003).

In most species, variation in body size influences both foraging ability and risk of predation (Werner & Hall 1988; Tripet & Perrin 1994; Aljetlawi, Sparrevik & Leonardsson 2004). To incorporate this size dependence, feeding rates may be defined using allometric functions that incorporate the effects of predator and/or prey body size with simple power laws (e.g. Kooijman 2000; Vucic-Pestic *et al.* 2010). These allometric functions take into account that a predator body size influences most aspects of its feeding behaviour. For example, size often determines the mobility and endurance of lizards affecting their ability to search for and pursue a prey (Le Galliard, Clobert & Ferrière 2004). Strength and bite force are also size-dependent and affect a lizard's ability to capture and handle prey (Herrel & O'reilly 2006). However, allometric functions often fail to incorporate density effects (but see Wahlstrom *et al.* 2000; Aljetlawi, Sparrevik & Leonardsson 2004; Vucic-Pestic *et al.* 2010) and ignore other relevant environmental effects (e.g. climate conditions in ectothermic vertebrates). Thus, both simple allometric relationships and classic functional response equations ignore the complexities in predator–prey interactions and make unrealistic assumptions about how predators consume resources (Brose 2010). Realistic estimates of feeding rates also require conducting experiments under natural conditions as laboratory experiments may not accurately reflect field behaviours (e.g. Witz 1996). Laboratory experiments often fail to capture ecological complexity in habitat structure, prey diversity and social dynamics, and these experiments frequently use model species that do not represent complex predators, such as most vertebrates. Unfortunately, direct observation of food acquisition in natural conditions is difficult and natural environmental variability often leads to noise and co-variation in data from field studies.

To circumvent these previous limitations of foraging ecology studies, it is important to conduct experiments in natural conditions to obtain realistic estimates that capture the effects of body size, density and climate conditions on the foraging success of diverse species. This study achieves this important goal by investigating natural feeding rates of the European common lizard *Zootoca vivipara* Jacquin (Fig. 1) in outdoor enclosures. *Z. vivipara* is a small ovoviviparous lizard that preys opportunistically on diverse invertebrate species (Avery 1966; see also Appendix S1, Supporting Information). Our goals were to: (i) gain an understanding of the factors influencing prey consumption in *Z. vivipara* by using a comprehensive approach that incorporates individual, population and environmental effects; (ii) identify the most parsimonious feeding rate function considering diverse allometric and density-dependent functions; and (iii) investi-



Fig. 1. Adult male of the species *Zootoca vivipara* (European common lizard) at an outdoor enclosure in the CEREEP, France (48°17'N, 2°41'E). Photo credit: M. González-Suárez.

gate the effect of varying lizard densities and thus, predation pressure, on the invertebrate community. The importance of our study hinges on exploring a novel comprehensive approach to define prey–predator interactions using field data from a complex vertebrate predator. Our results highlight the importance of exploring diverse approaches using field data to advance our understanding of foraging dynamics.

Materials and methods

LIZARD POPULATIONS: ENCLOSURES

During the summer of 2008, we established five experimental density treatments of *Z. vivipara* in 24 outdoor enclosures at the Centre de Recherche en Ecologie Expérimentale et Prédictive (CEREEP, 48°17'N, 2°41'E). Initial densities were equivalent to 700–3500 adults + yearlings per ha and sex ratios were close to 1 : 1. Surviving lizards ($n = 326$) from all treatments were recaptured in May–June 2009 (93% of recaptures occurred on 4 days in May) and a final population density (P) per enclosure was calculated. After capture, we estimated body mass for each lizard and classified female reproductive status as pregnant or non-pregnant. We also obtained an estimate of sunshine duration (I , in h day^{-1}) from a Campbell Scientific (Cortaboeuf, France) CSD3 solar radiation sensor located within 300 m of the enclosures. Sunshine duration is defined as total time with direct solar radiation exceeding 120 W m^{-2} (W.M.O. 2008) and was calculated over 10-min intervals. Although both air temperature and solar radiation influence activity in reptiles, based on previous studies we expected sunshine duration would influence activity (and hence, feeding) more directly than temperature in this species (Avery 1971; House, Taylor & Spellerberg 1980). Additional details of the enclosures, the density manipulation and lizard captures are provided in Appendix S1 (Supporting Information).

PREY POPULATIONS

Invertebrate abundance was estimated by a combination of pitfall trapping and sweep-net capture techniques (Brennan, Majer & Moir

2005) after all lizards had been captured to avoid injuries to the lizards, that is, drowning in a pit trap. Invertebrates were classified into order following Chinery (2005) and dried to determine dry biomass (in mg) per order in each enclosure. Estimated biomass represents an index as not all invertebrates in each enclosure were captured. We computed a total biomass index including all invertebrate groups, a preferred prey biomass index (N_p), which includes the orders Araneae, Homoptera, Heteroptera and Orthoptera (Avery 1966), and a spider biomass index (N_s , Araneae). Spiders were considered independently because they are the principal food of *Z. vivipara* (Avery 1966; Le Galliard, Ferrière & Clobert 2005a) and also were the most common invertebrate group in the enclosures (Fig. S1, Supporting Information). Additional details of the invertebrate captures are provided in Appendix S1 (Supporting Information).

ESTIMATION OF FEEDING RATES

We inferred natural feeding rates from measured faecal production using a standard relationship between faecal production and food consumption. This relationship was defined using data from a laboratory feeding experiment (see Appendix S1, Supporting Information). We measured faecal production for 107 lizards captured in the outdoor enclosures. After capture these lizards were housed in individual terraria and kept without food for 3 days. All faecal pellets produced since capture were dried and weighed. Using the experimental relationship between faecal production and food consumption we estimated natural feeding rates (in mg of live prey per day). Experimental procedures are described in more detail in Appendix S1 (Supporting Information).

DATA ANALYSIS: FEEDING RATES

Using the laboratory data, we explored several models aiming to predict faecal production from food intake (E). Some models included effects of S (sex as male or female) and/or M (lizard mass in g). The best fitting model was selected using an information-theoretic approach described below. The selected model was used to infer natural feeding rates from the measured faecal output of the animals captured in the outdoor enclosures.

We investigated the effects of predator body mass (M) and sex (S), predator (P) and prey (N) densities and sunshine duration (I) on the estimated natural feeding rates, applying allometric functions and functional responses. The simplest allometric function considered was $f(M) = AM^B$, in which feeding rates only depend on M . The allometric coefficient A and exponent B are estimated from the data. Alternative allometric functions were derived from this function by allowing the A and/or B parameter to vary between males and females, or introducing a linear effect of sunshine duration [e.g. $f(I, M) = AIM^B$]. In total, we explored 11 allometric functions.

In addition, we formulated a group of functional response models considering Holling type I and type II response models (Holling 1959) and a ratio dependent model (Hassell & Varley 1969). The type I response model assumes a linear increase in predation with increasing prey density (N), $f(N) = bN$, where b is the attack rate. The type II response model assumes an asymptotic relationship of feeding rate with prey density, $f(N) = \frac{bN}{1+bT_hN}$, where b is the attack rate and T_h the handling time. The Hassell–Varley flexible ratio function is a modified Holling type II model in which predation rate is influenced by prey (N) and predator density (P), $f(N, P) = \frac{b(N/P^m)}{1+bT_h(N/P^m)}$, where b is the attack rate, T_h the handling time and m an exponent that

determines the strength of the predator density effect. In all models, prey densities (N) were defined as either preferred prey biomass (N_p) or spider biomass (N_s).

These three basic functional response equations were modified to include more complex attack rates that incorporate effects of predator body mass and sex, as well as sunshine duration. Attack rates are expected to increase with predator size as larger lizards have greater sensory acuity and locomotor ability (Garland 1984). In *Z. vivipara* prey size has been observed to increase with lizard size (Avery 1966) and we used an allometric attack rate function $b(M) = b_1M^{b_2}$ where b_1 is an allometric coefficient and b_2 an allometric exponent. In some models we also included an effect of predator sex [e.g. $b(M, S) = b_1(S) \cdot M^{b_2(S)}$] and sunshine duration [e.g. $b(I, M) = b_1I \cdot M^{b_2}$]. Although handling time (T_h) may vary with body size (Persson *et al.* 1998), a recent study found these rates were relatively constant except for the smallest predators (Aljetlawi, Sparrevik & Leonardsson 2004). We therefore assumed that handling time is constant. In total, we explored 54 functional response models.

All models were fitted using the non-linear procedure NLS in R.2.10.0 (R Development Core Team 2009). The best fitting model(s) was selected using an information-theoretic approach (Burnham & Anderson 2002) considering Akaike's information criterion corrected for small sample sizes (AIC_c), model support as the difference in AIC_c between each model and the model with the lowest AIC_c (Δ), and AIC_c weight (w_i). Total w_i was calculated as the cumulative weight of all models including a particular variable or type of functional response (e.g. Holling type I response), which is similar to the variable weight w_j proposed by Burnham & Anderson (2002). All models with $\Delta < 2$ were considered to be supported. We also estimated the percentage deviance explained as (model deviance-null model deviance/null model deviance)-100, where the null model is an intercept only model.

DATA ANALYSIS: IMPACT ON INVERTEBRATE COMMUNITIES

First, we explored the relationship between invertebrate biomass index (total, N_p or N_s) and predator density (P) using linear regression. Secondly, we defined an invertebrate community similarity matrix among enclosures based on pairwise Bray–Curtis indices. Bray–Curtis indices were calculated as the absolute difference in invertebrate order biomass between two enclosures, summed over for all orders and divided by the total biomass in all enclosures and orders (Bray & Curtis 1957). To detect changes in community structure (biomass and composition) due to lizard density we used a test analogous to a multivariate analysis of variance called ADONIS (Oksanen *et al.* 2009). ADONIS returns a statistic R , which is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation), and a p -value estimated by repeated permutations of the data. We used the ADONIS procedures in the VEGAN package in R.2.10.0 (R Development Core Team 2009) with 999 permutations.

Although enclosures had overall similar habitat and environmental conditions, we expected a gradient of soil humidity due to differences in proximity to a nearby creek. Therefore, we introduced creek proximity, a proxy for humidity, as an additional regression variable to explain invertebrate biomass and as a block in the ADONIS procedure. Enclosures were distributed in five rows running more or less parallel to the creek, thus creek proximity was ranked from 1 to 5 with 1 assigned to the row of enclosures closest to the creek (~30 m) and 5 to those furthest (~90 m).

Results

EXPERIMENTAL RELATIONSHIP BETWEEN FEEDING RATE AND FAECAL PRODUCTION

The best model to explain faecal production includes only food intake (E). However, there were two additional models supported by the data (Table 1) that include mass and sex. At the time of this experiment, six females were in an advanced stage of pregnancy and ate considerably less than expected based on their body mass because their abdominal cavity was largely occupied by developing eggs. We repeated our analysis excluding these individuals and found that a single model, including only E , was supported (Table 1). Therefore, we used the function $faecal\ output = \beta \cdot E$ ($\beta = 0.072$, $SE = 0.006$, $p < 0.0001$, deviance explained = 29.7%), where E is in mg of live prey day^{-1} and $faecal\ output$ is a daily mean estimated over 3 days (dry mg day^{-1}).

NATURAL FEEDING RATES

All individuals captured in the field produced faeces, which indicate that all had eaten prior to capture. There was no effect of capture date on food intake (ANOVA $F_{3,105} = 2.15$, $p = 0.10$). Two females had a faecal output much larger than expected based on their body mass (see Fig. 2) and were identified as outliers during the analysis of the data. Reported results do not include these outliers because parameter estimates were different (particularly the allometric exponent) even though selected models were similar in both data sets. In the allometric function group, two models were supported while only three had $w_i > 10\%$ (Table 2). Both supported models include the same predictors: sex (S) and body mass (M); however, they differ in how the sex effect was introduced (either modifying the allometric coefficient A or the exponent B ; Table 3). Supported models were nearly identical in their AIC_c value and the resulting curves largely overlapped, predicting the highest feeding rates for larger female lizards (Table 3 and Fig. 2, deviance explained = 31.4%). Mean

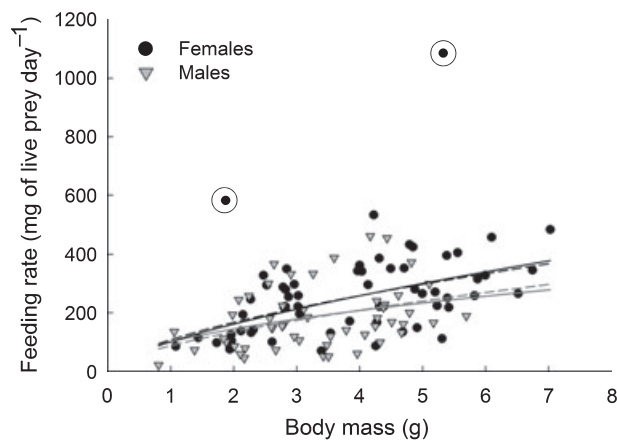


Fig. 2. Feeding rate as a function of body mass and sex in *Zootoca vivipara*. The two best supported models, which received nearly identical support (Table 2), are represented by solid (top model) and dashed lines (second model). Two identified outliers are circled and were not used to define the regression function.

(\pm SE) food intake was 182.68 ± 15.605 mg day^{-1} for males and 251.51 ± 15.135 mg day^{-1} for females. We found no differences between natural feeding rates of pregnant and non-pregnant females controlling for body mass (residuals of a mass model, Student $t = 0.75$, d.f. = 56, $p = 0.457$). Models including an effect of sunshine duration (I) received low support (total $w_i = 0.07$).

In the functional response group, two models were supported and only three models had $w_i > 10\%$ (Table 2). The top model was based on a Holling type II function for preferred prey biomass (N_p) with a M -, S - and I -dependent attack rate (Table 3). The second supported model also included a M -, S - and I -dependent attack rate but was based on a Hassell–Varley function (Table 3). However, the exponent m , which describes the effect of predator density, was not significantly different from zero (Table 3). It is important to note that we did not have cross-treatments in which both prey and predator densities were controlled and varied. As a result prey and predator densities were correlated

Table 1. Selection results of models exploring faecal output in *Zootoca vivipara* kept in the laboratory for the complete data set ($n = 41$) and for a data set excluding pregnant females ($n = 35$)

Faecal output model*	k	AIC_c	Δ	w_i	% deviance explained
All data					
$\beta \cdot E$	2	213.469	0.000	0.4741	29.705
$\beta(S) \cdot E$	3	214.788	1.318	0.2453	31.423
$\beta \cdot M^R \cdot E$	3	215.347	1.877	0.1854	30.482
$\beta(S) \cdot M^R \cdot E$	4	216.681	3.212	0.0952	32.369
Excluding pregnant females					
$\beta \cdot E$	2	182.276	0.000	0.5505	26.805
$\beta(S) \cdot E$	3	184.488	2.212	0.1822	27.599
$\beta \cdot M^R \cdot E$	3	184.293	2.017	0.2008	27.195
$\beta(S) \cdot M^R \cdot E$	4	186.504	4.228	0.0665	28.317

We report number of parameters (k), Akaike's information criteria (AIC_c), model support (Δ), model weights (w_i) and percentage deviance explained. Supported models are in bold.

*In the models: E = experimental food intake, M = lizard body mass, S = lizard sex. β is the allometric coefficient and R is the allometric exponent.

Table 2. Selection results of simple allometric functions and functional responses describing feeding rates under semi-natural conditions in *Zootoca vivipara*

Feeding rates model*	<i>k</i>	AIC _c	Δ	<i>w_i</i>	% deviance explained
Simple allometric functions					
<i>A</i> · <i>M</i> ^{<i>B</i>(<i>S</i>)}	4	1264·258	0·000	0·371	31·382
<i>A</i> (<i>S</i>) <i>M</i> ^{<i>B</i>}	4	1264·286	0·027	0·366	31·400
<i>A</i> (<i>S</i>) <i>M</i> ^{<i>B</i>(<i>S</i>)}	5	1266·388	2·130	0·128	31·450
<i>A</i> · <i>M</i> ^{<i>B</i>}	3	1267·814	3·556	0·063	27·560
<i>A</i> · <i>I</i> · <i>M</i> ^{<i>B</i>(<i>S</i>)}	4	1269·132	4·874	0·032	28·141
<i>A</i> (<i>S</i>)· <i>I</i> · <i>M</i> ^{<i>B</i>}	4	1269·413	5·155	0·028	27·948
<i>A</i> (<i>S</i>)· <i>I</i> · <i>M</i> ^{<i>B</i>(<i>S</i>)}	5	1271·321	7·063	0·011	28·152
Functional responses					
$\frac{b_1(S)I \cdot M^{b_2(S)} N_p}{1 + b_1(S)I \cdot M^{b_2(S)} T_h N_p}$	6	1267·204	0·000	0·325	32·380
$\frac{b_1 I \cdot M^{b_2(S)} N_p / P^m}{1 + b_1 I \cdot M^{b_2(S)} T_h N_p / P^m}$	6	1268·749	1·545	0·150	31·378
$\frac{b_1(S)I \cdot M^{b_2(S)} T_h N_p}{1 + b_1(S)I \cdot M^{b_2(S)} T_h N_p / P^m}$	7	1269·354	2·150	0·111	32·475
$\frac{b_1(S)I \cdot M^{b_2} N_p}{1 + b_1(S)I \cdot M^{b_2} T_h N_p}$	5	1269·581	2·376	0·099	29·333
$\frac{b_1 M^{b_2(S)} N_p}{1 + b_1 M^{b_2(S)} T_h N_p}$	5	1270·141	2·936	0·075	28·956
$\frac{b_1(S)M^{b_2(S)} N_p}{1 + b_1(S)M^{b_2(S)} T_h N_p}$	6	1270·812	3·608	0·053	30·016
$\frac{b_1 I \cdot M^{b_2(S)} N_s}{1 + b_1 I \cdot M^{b_2(S)} T_h N_s}$	5	1271·698	4·493	0·034	27·894

We present the top models with the number of parameters (*k*), Akaike’s information criteria (AIC_c), model support (Δ), model weights (*w_i*) and percentage deviance explained. Supported models are in bold.

**I* = sunshine duration, *N_p* = preferred prey biomass, *N_s* = spider biomass, *P* = lizard abundance, *M* = lizard body mass, *S* = lizard sex. *A*, *B*, *b₁* and *b₂* are allometric coefficients and exponents. The exponent *m* describes the strength of a predator density effect.

Table 3. Parameter estimates for the best models defining natural feeding rates in *Zootoca vivipara* considering simple allometric functions and functional responses

Feeding rates model*	Parameter ± SE [†]	<i>p</i>
Simple allometric functions		
<i>A</i> · <i>M</i> ^{<i>B</i>(<i>S</i>)}	<i>A</i> = 100·47 ± 18·050	<0·0001
	<i>B</i> _{fem} = 0·70 ± 0·119	<0·0001
	<i>B</i> _{male} = 0·52 ± 0·146	<0·001
	<i>B</i> = 0·63 ± 0·124	<0·0001
<i>A</i> (<i>S</i>) <i>M</i> ^{<i>B</i>}	<i>A</i> _{fem} = 107·85 ± 20·508	<0·0001
	<i>A</i> _{male} = 87·02 ± 15·259	<0·0001
	<i>B</i> = 0·63 ± 0·124	<0·0001
Functional responses		
$\frac{b_1(S)I \cdot M^{b_2(S)} N_p}{1 + b_1(S)I \cdot M^{b_2(S)} T_h N_p}$	<i>T_h</i> = 0·003 ± 0·0003	<0·0001
	<i>b</i> _{1fem} = 0·03 ± 0·043	0·448
	<i>b</i> _{1male} = 0·17 ± 0·100	0·098
	<i>b</i> _{2fem} = 3·58 ± 1·51	0·020
	<i>b</i> _{2male} = 1·28 ± 0·544	0·020
	<i>T_h</i> = 0·003 ± 0·0004	<0·0001
$\frac{b_1 I \cdot M^{b_2(S)} N_p / P^m}{1 + b_1 I \cdot M^{b_2(S)} T_h N_p / P^m}$	<i>b</i> ₁ = 0·17 ± 0·185	0·361
	<i>b</i> _{2fem} = 2·44 ± 0·825	0·004
	<i>b</i> _{2male} = 1·58 ± 0·600	0·009
	<i>m</i> = 0·03 ± 0·290	0·907

See Table 2 for model selection.

**I* = sunshine duration, *N_p* = preferred prey biomass, *N_s* = spider biomass, *P* = lizard abundance, *M* = lizard body mass, *S* = lizard sex.

†Subscripts indicate fem: parameter value for females, male: parameter value for males.

(*P*-*N_p* Pearson *r* = −0·69, *P*-*N_s* *r* = −0·56) and parameters in the Hassell–Varley models may not have been estimated adequately.

Overall, models based on a Holling type II response had more support (total *w_i* = 0·65) than those based on the Hassell–Varley function (total *w_i* = 0·34), while Holling type I response models received no support (total *w_i* < 0·0001). Models based on *N_p* had higher weights (total *w_i* = 0·89) than models based on spider biomass only (*N_s*; total *w_i* = 0·11). Models including *M*- and *S*-dependent attack rates were strongly supported (total *w_i* > 0·99 and total *w_i* = 0·98, respectively). In contrast to the results from the allometric group, functional response models including an effect of *I* were supported (total *w_i* = 0·79). Density-dependent models not including individual traits (*M* and *S*) received no support (Δ > 34·34, *w_i* < 0·0001).

Because both groups of models used the same data base, we could also compare them to determine the most parsimonious model overall. The top two allometric functions including *S* and *M* (Tables 2 and 3) were identified as the only supported models when combining both groups of functions. The best functional response model had Δ = 4·5 (Table 2), suggesting limited support for a density effect on natural feeding rates.

IMPACTS OF LIZARD DENSITY ON INVERTEBRATE POPULATIONS

We captured and identified invertebrates from 17 different orders. The most abundant group was Araneae (Fig. S1, Supporting Information), while Ephemeroptera, Neuroptera and Odonata were rare (found in less than six enclosures and representing <0·5% of the total biomass). There was no

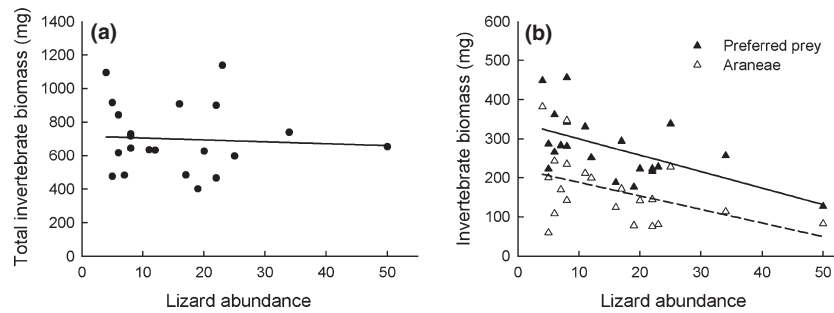


Fig. 3. Invertebrate biomass and lizard abundance on 21 outdoor experimental enclosures. (a) Total invertebrate biomass. (b) Preferred lizard prey (orders: Araneae, Heteroptera, Homoptera and Orthoptera), and spider biomass (Araneae). Note different scale of the y-axis.

relationship between the total invertebrate biomass index and lizard density or creek proximity ($F_{5,15} = 2.00$, $p = 0.14$; adjusted $R^2 = 0.20$; Fig. 3a). However, we found a significant negative effect of lizard density on biomass of preferred lizard prey (N_p , $\beta = -3.29$, $SE = 1.305$; Fig. 3b) with no effect of creek proximity (overall regression $F_{5,15} = 4.84$, $p = 0.008$, adjusted $R^2 = 0.49$). There was also an effect of lizard density on spider biomass (N_s , $\beta = -1.69$, $SE = 1.393$; Fig. 3b) with no effect of creek proximity (overall regression $F_{5,15} = 4.49$, $p = 0.011$, adjusted $R^2 = 0.47$). Despite these differences for particular invertebrate groups, we did not detect differences in invertebrate community structure with lizard density, although there was a weak but significant effect of creek proximity (density: $R = 0.05$, $p = 0.38$; creek proximity: $R = 0.14$, $p = 0.05$). Results did not change if the rare orders: Ephemeroptera, Neuroptera and Odonata, were excluded.

Discussion

INTRINSIC FACTORS INFLUENCING FEEDING RATES

Both lizard body mass and sex had important effects on individual feeding rates. Larger predators consume more prey than smaller individuals as previously reported for *Z. vivipara* (Avery 1971; Pilorge 1982) and many other species (Tripet & Perrin 1994; Aljetlawi, Sparrevik & Leonardsson 2004; Vucic-Pestic *et al.* 2010). A new finding is that females consume greater amounts of food than males, even after controlling for differences in body mass. Previous studies of *Z. vivipara* failed to detect (Avery 1971) or to consider (Van Damme, Bauwens & Verheyen 1991) these sex differences. However, our results suggest they may be important.

There are several possible non-exclusive explanations for these sex differences. Females could have increased feeding rates to compensate for their recent investment in reproduction (Avery 1974). However, we found that pregnant and non-pregnant females had similar feeding rates. Alternatively males may spend less time foraging because they engage in reproductive behaviours during this time of the year. On the other hand, females and males may have different diets due to distinct energy requirements and investment strategies. For example, juvenile female *Z. vivipara* invest more in body length growth, while males invest in body condition (mass

adjusted for length, Le Galliard, Ferrière & Clobert 2005b). Whether these differences in energy investments influence feeding rates remains to be determined.

EXTRINSIC FACTORS INFLUENCING FEEDING RATES AND FUNCTIONAL RESPONSE FUNCTIONS

Feeding rates generally increase with sunshine duration (see also Avery 1971; House, Taylor & Spellerberg 1980). However, the effect of sunshine was only noticeable within the functional response model group, suggesting attack rates (search and detection of prey) increase in sunnier days. Future experimental studies may be necessary to clarify the role of weather conditions in *Z. vivipara* feeding rates. Similarly, evidence of prey density effects in feeding rates was limited. Prey densities in semi-natural conditions cannot be easily manipulated. Instead prey biomass was expected to vary due to the experimental manipulation of lizard density. Although variability in prey was observed, there was only a weak effect of prey density in feeding rates. It is possible that prey densities remained sufficiently high to prevent strong food limitation even at the highest lizard densities.

Which functional response models better represent natural dynamics is a debated issue that this study directly addresses (Abrams & Ginzburg 2000; Schenk, Bersier & Bacher 2005). We found best support for a Holling type II functional response in *Z. vivipara* suggesting feeding rates reach a limit at high prey densities. However, unlikely previous studies (Schenk, Bersier & Bacher 2005; Miller *et al.* 2006), we only found limited support for an effect of predator density. The common lizard is a non-territorial species with overlapping home ranges and conspecific interference during predation may be rare (Massot *et al.* 1992). Alternatively, the correlation between prey and predator densities may have limited our ability to correctly fit models including both density effects.

MOST PARSIMONIOUS FEEDING RATE FUNCTIONS

A primary goal of this study was to identify the most parsimonious feeding rate function following a comprehensive approach that includes both allometric and functional responses. Many studies consider only one group of models and thus create a dichotomy that does not exist in reality

(Brose 2010). Our results show that both prey density and body mass influence feeding rates, but that individual traits, mass and sex, are much better predictors. Recent studies have shown the importance of considering both density and body mass effects and have suggested the use of allometric functional response models in which attack rates and/or handling times are size dependent (Aljetlawi, Sparrevik & Leonardsson 2004; Vucic-Pestic *et al.* 2010). Allometric functional responses provide an important tool to represent individual and population level effects (Brose 2010). However, for empirical studies and generalist predators, simpler allometric functions may provide a more parsimonious description of the data than complex allometric functional response models. Even though at some level prey density must affect feeding rates and functional response models are an important contribution to the field of ecology (Abrams 2000), variation in prey consumption may be better explained by individual differences than by natural variation in prey density. In light of these results, we urge researchers to explore diverse types of function, including allometric functional responses and simpler functions, while considering the effects of multiple individual traits such as mass and sex, prey and predator population densities, and whenever possible environmental variables.

Despite a weak effect of prey density on consumption rates, our study documents a negative effect of lizard density on preferred prey and in particular on spider biomass, presumably as a consequence of feeding pressure. A negative effect of lizard density on spider abundance has been previously reported (Spiller & Schoener 1998; Le Galliard, Ferrière & Clobert 2005a). This effect may be potentially important for community diversity and structure because spiders are themselves predators that can influence other invertebrates and habitat conditions (Greenstone 1999; Schmitz 2008). Therefore, lizards could directly, via predation, and indirectly, via their effect on spiders, influence the composition and biomass of the invertebrate communities (Spiller & Schoener 1998). Although in our study we did not find a significant effect of lizard density on invertebrate community structure, which instead appears to respond to creek proximity (a proxy of humidity), effects may occur at different densities of lizards and/or spiders.

One caveat in our study is that prey and lizard densities could not be estimated at the same time. This time-lag may have limited our ability to identify existing effects of prey density on lizard feeding rates or of lizard density on prey communities. Regrettably, we could not estimate prey biomass until after all lizards were captured to avoid injuring lizards inside insect traps and thus, we could not estimate prey and lizard densities simultaneously. These difficulties are drawbacks of field studies. Nevertheless, we detected an expected effect of lizard density on prey abundance, suggesting measured prey densities did reflect, at least to some extent, enclosure conditions prior to lizard removal.

Finally, the observation that prey consumption depends only weakly on prey density is both interesting and puzzling. This result poses the question of how common lizard popula-

tions and their prey are regulated (Massot *et al.* 1992; Abrams 2000). If populations are regulated through prey depletion as typically assumed in population dynamic models, prey consumption should decrease with predator density due to a decrease in prey abundance. We indeed found a negative effect of lizard density on preferred prey and spider biomass. However, the associated reduction in predation rate was less evident. This might imply that other ecological interactions, which remain unexplored, are involved in the regulation of these lizard populations.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Extended methods.

Fig. S1. Total invertebrate biomass per experimental enclosure.

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