From set menu to *a la carte*. Linking issues in trophic ecology of Mediterranean lacertids

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ABSTRACT

Lacertids are the dominant group of lizards throughout the Mediterranean Basin. Their role in food web transfer of matter and energy from arthropods and other small invertebrates to birds and mammals constitutes a major function within Mediterranean ecosystems. For many years, prey consumption by lacertids was thought to be almost indiscriminate, not much more than a by-product of habitat use. However, increasing evidence does not support this passive view. Analyses of prey availability have revealed active prey selection/avoidance in several species. Others show an internal tendency (i.e., historical constraints) to consume specific animal items (ants, clumped prey) or plant matter (seeds, nectar, pollen, leaves). Behavioural experiments showed that lacertids not only identify different prey types by both visual and chemical cues but also modify their feeding behaviour integrating past experiences. Furthermore, size, sex, reproductive state, body condition, tail loss and probably other lizard features are relevant for feeding ecology. However, less attention has been devoted to abiotic factors such as temperature and humidity. More experimental studies of the influences of competitors, predators and parasites on diet are needed. Even though it is controversial, optimal foraging theory provides a conceptual background for future studies. The evolutionary history of the various lacertid lineages, which constrains their morphology and physiology and eventually produces exaptative traits, is to be considered as well. Finally, methodology in field sampling, lab work and statistical analysis needs to be developed. Recommendations are given as to when and where to sample, which compartment should be analysed, which is the appropriate sample size, how to assess trophic availability, which statistical descriptors should be used and how they should be compared.

KEY WORDS: Lacertidae - Trophic ecology - Prey selection - Herbivory - Optimal foraging - Experience - Historical constraints.

INTRODUCTION

Lacertids are the dominant group of lizards in the Mediterranean Basin both in number of individuals and in species richness. Despite the relatively small area, an amazing number of members of this family occur in this region (about 140 out of the 276 currently recognised species, EMBL, 2002). The intermediate position between three continents, the great heterogeneity of climates and habitats, the complex geological history with multiple events of vicariance and dispersal are factors that explain this flourishing biodiversity (Arnold, 1989; Böhme & Corti, 1993). Furthermore, the time-for-speciation factor should be taken into account (Stephens & Wiens, 2003): the whole family probably originated in the Mediterranean area (Estes, 1983; Arnold, 1989) and remained there during the Early Cenozoic. The most basal branches in the lacertid phylogeny are clearly restricted to the Western Palearctic (Harris *et al.*, 1998).

As a result of this ecological and historical context, few vertebrates are so common and successful in Mediterranean environments. One or more species are present in high mountains, hills and coastal plains, peatbogs, rock outcrops, clearings and borders of deciduous and evergreen forests, scrublands, steppes, coastal dunes, sandy and rocky deserts, big islands and tiny islets, and even agricultural fields and human settlements (Arnold, 1989). In these diverse habitats they prey upon an enormous variety of arthropods and other small invertebrates and, in some cases, other vertebrates and plant matter. They are preyed on by raptors, corvids, seagulls, carnivorous mammals and snakes (Martín & López, 1996; Schleich *et al.*, 1996; Barbadillo *et al.*; 1999; Maslak & Pasko, 1999; Corti & Lo Cascio, 2002). Small species are even consumed by bigger ones (Castilla *et al.*, 1991).

This intermediate role in food webs transferring matter and energy from invertebrates to endothermal vertebrates constitutes a major function in Mediterranean ecosystems (Valverde, 1967). As stated by Margalef (1991) the mean energy transfer between nodes in trophic webs is only about 10%, the same found specifically in ectothermal vertebrates (Townsend *et al.*, 2002). Unlike the human concept, this 'inefficiency' mostly derives from the shift of energy to other more complex activities and regulates and promotes diversification at both higher and lower trophic levels (Townsend *et al.*, 2002). An ecosystem without lacertids (or other equivalent key species) would support very poor communities of arthropods and carnivorous vertebrates. Thus, the analysis of present and future studies on the trophic ecology of lacertids (the aim of this review) is not a restricted topic, but concerns a substantial part of Mediterranean ecosystems and their evolutionary history.

PREY CONSUMPTION AND CONSTRAINTS

Studies describing the diet of lacertids are numerous, most are included in the review by Van Damme (1999).

Almost all Orders of Arthropoda, some Gastropoda, very small vertebrates and even some plant elements can be consumed by lacertids. Most species (but not all) are active foragers and show generalist diets with no apparent specialisations (Díaz, 1995). Although studies vary in method greatly, their general findings are that the diet of a species changes with the size (and sometimes sex) of the lizard, season and site within the same species. However, different species analysed in the same place and time do not consume exactly the same prey. As for many years, prey consumption by lacertids was thought to be almost indiscriminate (Avery, 1966; Arnold, 1987; Mou, 1987), this intra- and interspecific variation was interpreted as a secondary consequence of changes in prey availability between (micro) habitats used by different species and classes (Arnold, 1987; Capula & Luiselli, 1994) or between different seasons.

The only exception admitted was the constraints derived from morphology (i.e., gape) and its functional derivations (i.e., bite force). As a rule, within a species, juvenile lacertids do not eat the biggest items consumed by adults which, however, do not neglect small prey. As a result, the distribution of prey sizes consumed follows a logarithmic pattern, with juveniles differing from adults in modal values (Fig. 1). This has been interpreted as lack of selection in prey size (Pianka, 1986). Correlation between lizard and prey sizes is usually weak and variance explained increases only when the biggest prey consumed by individual is considered (Fig. 1). As male lacertids have larger heads that females of the same size (Arnold, 1987), they are expected to consume relatively larger prey. Big heads primarily evolved as a result of sexual selection for male-male combat and female holding during copulation (Olsson & Madsen, 1999; Herrel et al., 1996). However, increased gape and bite force undoubtedly spread the food spectrum mechanically available for males (Herrel et al., 1999, 2001) and natural selection could contribute to maintaining or increasing this dimorphism in order to decrease trophic competition between sexes if food resources were restricted.

In contrast with other lizard groups (Pérez-Mellado & De la Riva, 1993; Perry, 1996), evidence of trophic niche divergence between sexes in lacertids is limited. Although male Gallotia galloti were able to crush harder prey than females in the lab, both sexes exceeded the bite force required for eating the usual prey (Herrel et al., 1999). Furthermore, male Lacerta (Zootoca) vivipara ate in the field some extremely large prey not consumed by females (Roig J. M. et al., 1998, Abstract in III Int. Symp. Lacertids of Mediterranean Basin, Cres, Croatia: 70), but the food spectrum of both sexes remained essentially the same (Fig. 1).

Similar constraints may also explain some interspecific differences in diet. Contribution of hard prey such as Coleoptera tends to increase with snout vent length (SVL) in lacertids at species level (Araujo, 1990, M.D. dissertation, University of Lisbon; Carretero & Llorente, 1991) and species of similar SVL but different head size

differed in their consumption of hard prey (Herrel et al., 2001; Verwaijen et al., 2002). However, there is no clear direct relationship between prey and predator sizes across species. For instance, Acanthodactylus erythrurus was bigger but ate smaller prey than sympatric Psammodromus algirus (Carretero & Llorente, 1993) and Podarcis pityusensis and P. hispanica living together consumed similar prey sizes although the former was much bigger (Carretero & Llorente, 2001).

PREY SELECTION

Microhabitat and seasonal heterogeneity of potential prey, along with morphological constraints, are, nevertheless, insufficient to explain the patterns of diet variation observed in lacertids. Increasing evidence supports prey selection (Heulin, 1986; Pollo & Pérez-Mellado, 1988; Díaz & Carrascal, 1990, 1993; Domínguez & Salvador, 1990; Pérez-Mellado et al., 1991; Gil et al., 1993).

All species studied ate prey sizes in different proportion as available but some shifted to bigger sizes (Díaz & Carrascal, 1990; Domínguez & Salvador, 1990; Gil et al., 1993) whereas others took smaller ones (Roig J. M. et al., 1998, Abstract in III Int. Symp. Lacertids of Mediterranean Basin. Cres, Croatia: 70). Prey taxa were also subject to selection, but the same divergent patterns were observed. For instance, ants were rejected by P. algirus, L. schreiberi, L. monticola, L. (Z.) vivipara and Podarcis bocagei (Díaz & Carrascal, 1990; Domínguez & Salvador, 1990; Pérez-Mellado et al., 1991), but positively selected by P. hispanicus and A. erythrurus, (Pollo & Pérez-Mellado, 1988; Gil et al., 1993).

In the framework of foraging theory (Schoener, 1971; Stephens & Krebs, 1986), Díaz (1995) enumerated five major factors involved in foraging choice by lacertids: time constraints, movement minimisation, nutrient optimisation, predation risk and body temperature, although others could probably be added. The lack of correlation between prey size and profitability (energy input/ handling time) within and between taxa suggest that, even for those species selecting for bigger prey, lacertids are not simply maximising energy intake (Díaz & Carrascal, 1993). When size is excluded, soft, rounded prey are more profitable than elongated, heavily chitinised ones (Díaz & Carrascal, 1993) because the handling time involved is lower.

In the Mediterranean regions, not only lizards' prey availability but also their time budgets may suffer strong seasonal changes. In P. algirus from Central Spain, adults tended to eat small prey in early spring and large in midsummer (Díaz & Carrascal, 1993). This result was interpreted as a shift in foraging priorities in line with the phenology of this species (Díaz et al., 1994; Díaz, 1995). At the beginning of the breeding season, lizards minimise handling time by eating small but profitable prey because at this time they are involved in non-foraging activities (home range defence, agonistic interac-
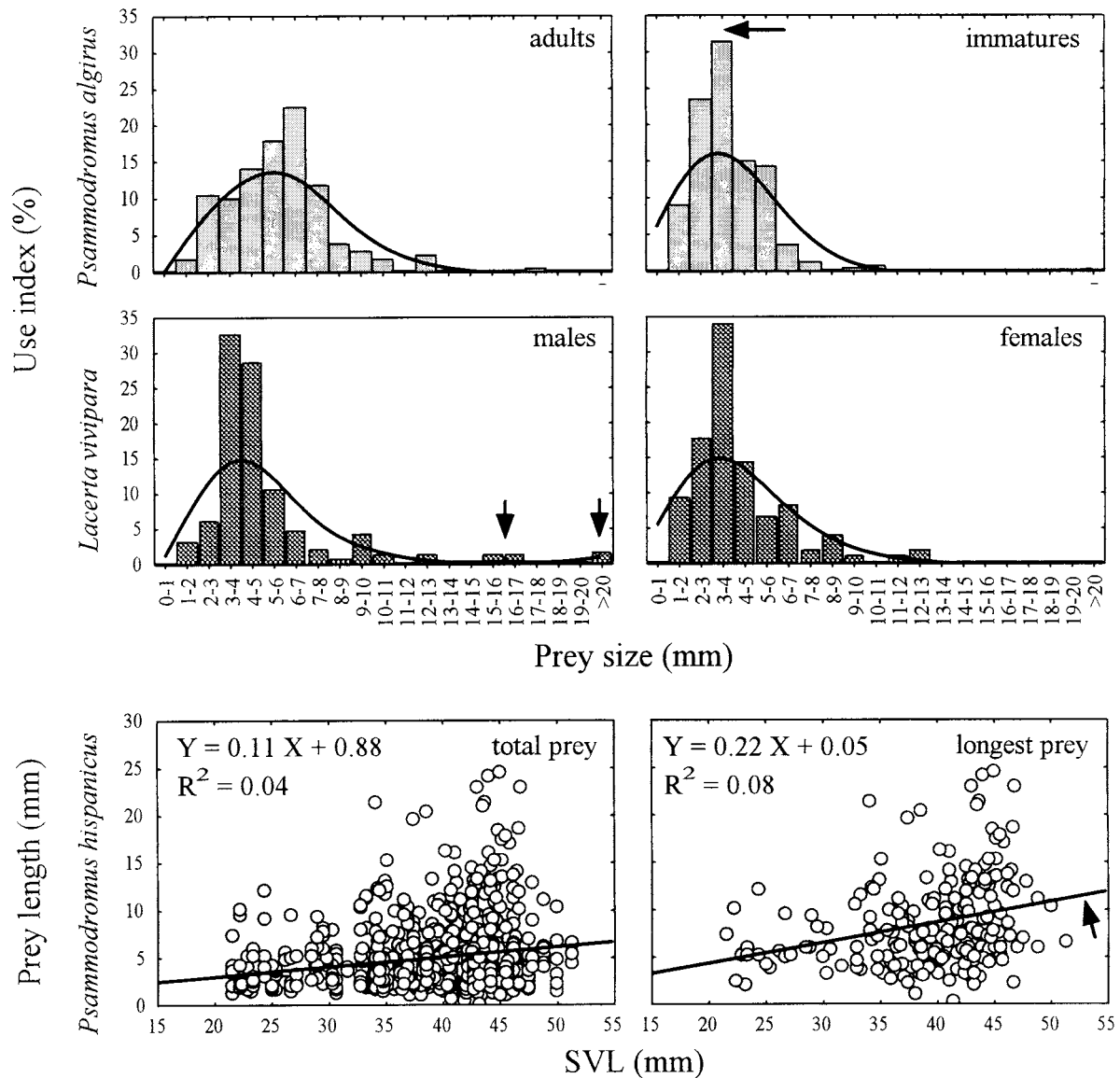
Fig. 1 - Prey size variation in three species of lacertid lizards. Above: distribution of prey sizes in adult and immature *Psammodromus algirus* from the NE Spanish coast. Middle: distribution of prey sizes in adult males and females *Lacerta* (*Zootoca*) *vivipara* from the Pyrenees. Below: relationships between lizard (SVL) and prey sizes in *P. hispanicus* from the NE Spanish coast (Carretero & Llorente, 1991). Left, total prey; right, maximum prey in every stomach content. Arrows point out the main differences.

tions, mate searching and guarding). However, once re-production finishes, they maximise energy input and minimise movement by taking few, big prey in order to recover reserves for the following season whilst reducing predation risk. Unfortunately, such pattern cannot be generalised. Neither territoriality nor extreme seasonality of *P. algirus* in Central Spain (Díaz *et al.*, 1994; Salvador & Veiga, 2001) can be extended to the coastal populations of this species (Carretero & Llorente 1997; Carretero 2002) which could have different foraging patterns. Moreover, similar analysis in non-territorial *L.* (*Z.*) *vivipara* in the Pyrenees did not reveal differences between breeding and non-breeding seasons (Roig J. M. *et al.*, 1998, *Abstract* in III Int. Symp. Lacertids of Mediterranean Basin. Cres, Croatia: 70), probably indi-

cating that adult common lizards devoted less time to breeding activities and/or that they were less constrained by food and predators.

The seasonal dimension of selection (not only for adults) appears then as a fundamental tool for determining foraging patterns (Fig. 2). In the three studies on lacertids giving this information (Pérez-Mellado *et al.*, 1991; Díaz & Carrascal, 1993), diet diversity tended to remain constant although diversity of available prey fluctuated seasonally (Fig. 2). Some of the main taxa consumed appeared in similar proportions throughout seasons ('warranty prey', Carretero & Llorente 1991, 1993) and the electivity of such prey was correlated inversely with their abundance (Fig. 2). This result is not expected for time optimisation (positive correlation) or
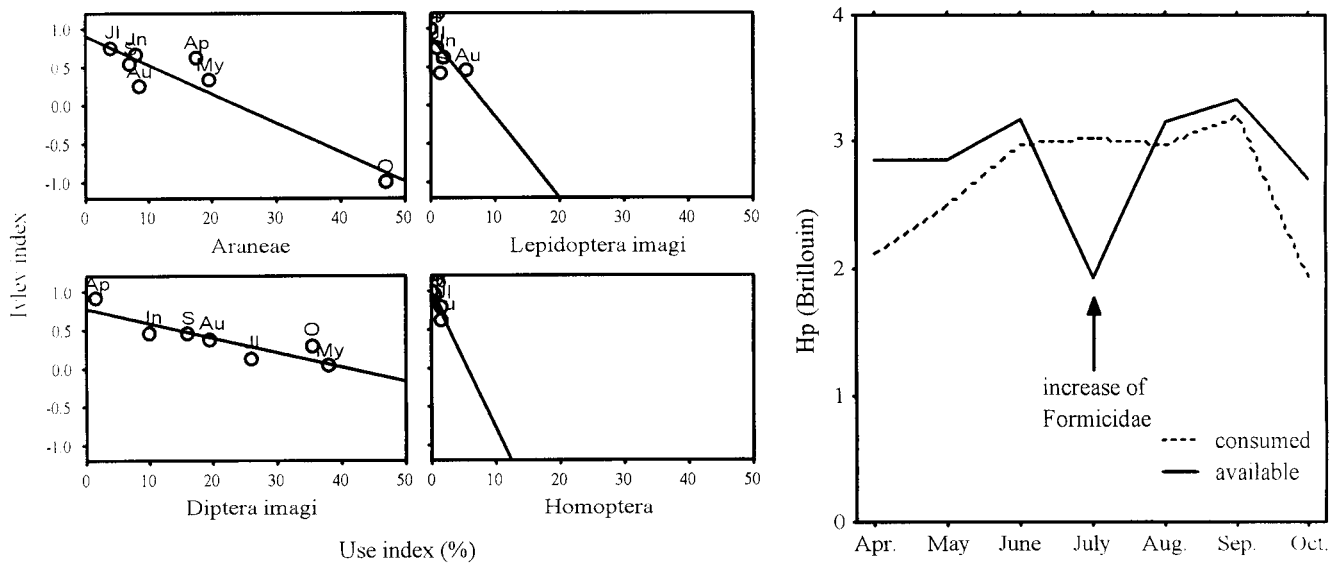
Fig. 2 - Evidence for trophic selection (and nutrient constraint) in a Pyrenean population of *Lacerta* (*Zootoca*) *vivipara*. Left, negative correlation between abundance and electivity of four major prey throughout the year; right, trophic diversity 'buffers' the seasonal variations of available diversity.

energy optimisation (non-negative correlation) strategies and strongly suggests the existence of nutrient constraints (Stamps *et al.*, 1981; Pérez-Mellado *et al.*, 1991). Alternatively, avoidance of toxins in various preys gives similar results, but these are more reliable for herbivorous lizards (Dearing & Schall, 1992; see below). Further studies should test these hypotheses by investigating the nutrients contents in different prey types (Pérez-Mellado *et al.*, 1991; Díaz, 1995; Rocha, 2000).

As mentioned above, predation risk can be an important factor conditioning lacertid behaviour, including foraging (Cooper, 2000; Martín, 2002, and references therein). When increasing the vulnerability of *L. monticola* to predators by experimental tail removal, lizards shifted to less exposed microhabitats with lower prey abundance and ate prey involving short handling time (Martín & Salvador, 1993). In another experiment, tailless *P. algirus* delayed attacking prey once it was perceived, which suggested conservative behaviour (Martín & Avery, 1997). Similar patters are also expected for pregnant females which are slower (Van Damme *et al.*, 1989), more sensitive to predation (Bauwens & Thoen, 1981) and remain closer to shelters (Braña, 1993).

As in other ectotherms, foraging in lacertids is also a temperature-dependent activity. This applies not only to quantitative effects on prey handling, gut passage and digestive efficiency (Avery *et al.*, 1982; Avery & Mynott 1990; Van Damme *et al.*, 1991), but also to the qualitative 'decisions' when attacking prey (Van Damme *et al.*, 1991, Díaz, 1994). For instance, when temperature increased *L.* (*Z.*) *vivipara* took larger and faster prey (Avery *et al.*, 1982, Van Damme *et al.*, 1991) and *P. algirus* tended to attack winged flies faster with more capture success (Díaz, 1994). At the interspecific level, Belliure *et al.* (1996) indicated covariation between thermal

ecology and foraging mode in two sympatric species: *P. algirus* showed less thermal inertia and basked more often, but for shorter periods as it was more active forager than *A. erythrurus*. Studies on thermal selection between lacertids and their prey can be very fruitful (Wehner *et al.*, 1992).

MECHANISMS FOR PREY SELECTION

Although prey selection itself seems well demonstrated, the proximal mechanisms involved still need to be determined. As a necessary condition for prey selection, Lacertids should be able to recognise different prey types, to evaluate their characteristics and to use this information to modify their foraging behaviour in function of their needs. Only recently, experiments have shown that lacertids identify different prey types both by visual and chemical cues (Desfilis *et al.*, 1993; Desfilis E., 1999, Ph.D. Thesis, University of Valencia; Cooper & Pérez-Mellado, 2001a, b, c, d, 2002) and that they are able to assess prey size (Díaz & Carrascal, 1990, 1993).

Juveniles of many lizard families are able to recognise, attack and consume prey items soon after hatching without previous experience (Burghardt, 1973; Reznik *et al.*, 1981), as expected from natural selection since parental food dependence is usually null. Since chemical patterns of different prey are probably very variable, this innate preference of lacertids (and many other lizards) probably corresponds to visual images of a small, moving object with an elongated shape (Desfilis & Font, 2002, personal communication). The traditional view extended this finding to every aspect of lizards' foraging behaviour, considering it as stereotyped (Burghardt, 1977). However, with some constraints,

these preferences can be modified by integration of experiences throughout the lizards' life, as demonstrated in numerous papers (see reviews by Burghardt, 1977; Desfilis & Font, 2002). This could even be extended to embryos (at least in viviparous species with maternal contacts) which are also sensitive to chemical environment and show modified behaviours after hatchling (Downes & Shine, 1999).

The selective advantages of learning processes in generalist species such as lacertids are clear. By using recent experience to modify foraging behaviour, they could avoid noxious prey, assess prey quality, increase predatory efficiency (detection, attack, handling), evaluate external constraints and, simultaneously, remain flexible to environmental changes in prey availability (Desfilis & Font, 2002). In the short term, experience with *P. hispanica* demonstrates that this species detects new prey through visual and chemical traits, but uses only visual detection when it has had previous contacts with the prey (Desfilis *et al.*, 1993; Desfilis E., 1999, Ph.D. Thesis, University of Valencia). In the long term, although no experiments have been carried out, learning explains reliably patterns of size selection and seasonally balanced diets previously reported (Pérez-Mellado *et al.*, 1991; Díaz & Carrascal, 1993). The comparative weight of stereotyped prey selection or learning changes across species is more important in those species with specialised diets (see below).

HERBIVORY

Partial or total shift to plant consumption represents a major change in lacertid trophic ecology. Several constraints make herbivory less widespread in lizards than in other reptiles (King, 1996; Cooper & Vitt, 2002). In physiological terms, plant matter provides less energy content than animal items and can only be digested efficiently if stored in great amounts decomposed by fermentative flora over a long period (King, 1996). Thus, it usually becomes restricted to species with large body size and lower metabolic rates (Pough, 1973). Anatomically, the streptostylic mandibular suspension of lizards precludes chewing (Ostrom, 1963) and limits the hardness and size of plant tissues consumed (King, 1996). A third, historical factor has been particularly applied to lacertids since herbivory and the family itself seem too recent to cause very thorough specialisations (Pérez-Mellado & Traveset, 1999).

At any rate, some species/populations mainly around the Mediterranean, in fact, consume large amounts of plant matter (see review by Pérez-Mellado & Traveset, 1999). Although there is general agreement on the plesiomorphic condition of arthropodivory in lacertids (Pérez-Mellado & Traveset, 1999), separate evolutionary lineages have shifted to herbivory to different degrees (all *Gallotia*, species or populations of *Lacerta*, *Psammodromus* and *Podarcis*) whereas others have not

(*Acanthodactylus, Algyroides, Mesalina, Ophisops*). Different species eat various plant portions: pollen, nectar, flowers, fruit pulp, seeds and plant fibres (Pérez-Mellado & Corti, 1993; Pérez-Mellado & Traveset, 1999).

Several traits have allowed lacertid lizards to bypass the theoretical constraints expounded above. Lacertids are able to pierce plant tissues in the same way as they do with animal prey (Herrel *et al.*, 1998); some become large (*Gallotia, Lacerta*) and develop jaw muscles strong enough to crush hard plant items (Herrel *et al.*, 1999); and the energetic and nutrient contents of plant reproductive organs are much higher than the vegetative parts (Pérez-Mellado & Corti, 1993). Moreover, some environmental conditions, particularly low predation pressure, increase the profitability of plant matter by decreasing its associate costs (see Selection section). This reasoning was used to explain the high frequency of herbivory on islands (Pérez-Mellado & Corti, 1993) (Fig. 3).

Both insularity and lizard size hypotheses have been simultaneously tested on an extensive data set of species, statistically excluding the historical effects (Van Damme, 1999). Though based in a questionable herbivore/carnivore dichotomy, conclusions of this meta-analysis only support the insularity hypothesis. Mainland-island and arthropodivory-herbivory transitions are associated; herbivorous lineages in the mainland are better island colonisers; herbivorous species are larger than arthropodivorous ones, but there is considerable overlap; and no body size differences between mainland and islands were found. Furthermore, a quantitative analysis of the proportion of plant matter in diet (Pérez-Mellado & Traveset, 1999) indicated that insularity was responsible for the high incidence of herbivory in the Mediterranean. Nevertheless, plant consumption by insular lacertids is heterogeneous. Some species/populations living in the
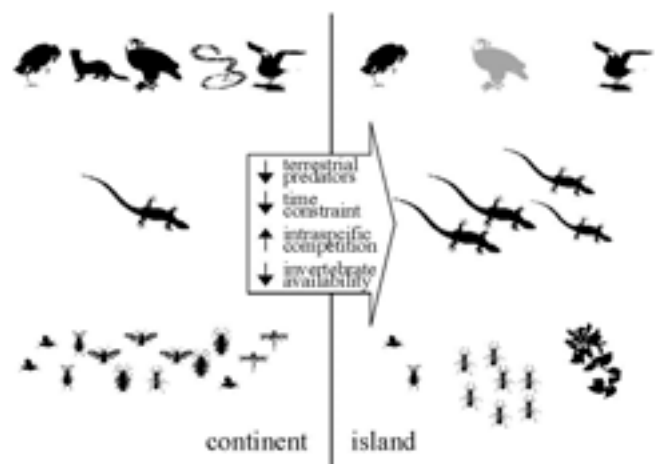

Fig. 3 - Diagram of the hypothesis of Pérez-Mellado & Corti (1993) on the herbivory of insular lacertids. In islands, lizards have fewer terrestrial predators, attain high densities but face high intraspecific competition and low arthropod availability. Consequently, they shift their diet to consumption of plant matter and clumped prey.

Mediterranean area are not herbivorous at all (Pérez-Mellado & Traveset, 1999). Others are omnivorous tending to consume more plant matter in summer or when increasing in size (Pérez-Mellado & Corti, 1993; Carretero *et al.*, 2001). Finally, others are almost completely herbivorous at the adult stage (Molina-Borja, 1986; Valido & Nogales, 1994; Pérez-Mellado *et al.*, 1999).

Pérez-Mellado & Traveset (1999) considered that (partial) herbivory in Balearic species does not represent true specialisation based on typical animal helminth communities and lack of apparent morphological adaptations. However, it must be remarked that the most herbivorous lineage, *Gallotia*, shows a typical herbivorous elements in its parasitofauna (Roca, 1999; Roca *et al.*, manuscript submitted). Moreover, greater gut size could mean a morphological adaptation to herbivory by increasing food storage and retention time. Ontogenic, allometric variation in relative gut size (Carretero, 1997, Fig. 3), together with jaw musculature and bite force (Herrel *et al.*, 1999), are anatomical constraints for juveniles which remain arthropodivorous even in herbivorous species. Intraspecific gut-size differences were also found in an earlier study (Carretero, 1997, Fig. 4), but the effects of adaptive and historical factors could not be disentangled. A new analysis of 11 species (including a Balearic one) corrected for phylogeny revealed significant positive correlation between gut size and proportion of plant matter in the diet (Carretero M. A. *et al.*, 1999, *Abstract* in X Meeting S.E.H., Irakleio, Greece, pp. 41-42) (Fig. 5). Although not included in the analyses, Canarian *Gallotia* show indeed deeper intestine adaptations with the presence of a rectal caecum (Roca V., unpublished data). This compartmentalisation is an alternative evolutionary path in order to increase food storage and retention (King, 1996).
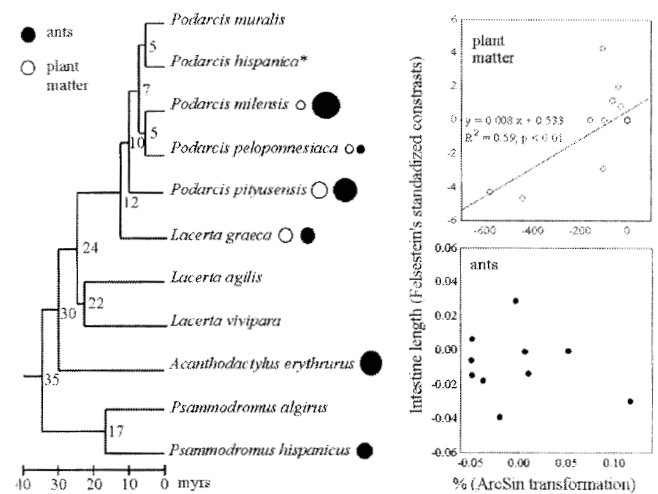
Fig 5 - Analysis of 11 lacertid species using phylogenetically independent contrasts (Felsestein, 1985; Garland, 1992) shows that gut size and plant consumption correlate, but ant consumption does not (Carretero *et al.*, 1999). Phylogeny used is based in Harris & Arnold (1999) and Harris *et al.* (1998).

Other evidence is that insular *P. pityusensis* introduced in a continental site remained partially herbivore, whereas syntopic continental *P. hispanica* did not consume plant matter (Carretero *et al.* 2001). Recent behavioural experiments have shown that herbivorous species are sensitive to chemical cues from plants they usually eat (Cooper & Pérez-Mellado, 2001b, c, d). Moreover, close mutualistic relationships between lacertids and plants (pollination, seed dispersal) have been developed in Balearic and Canarian lacertids, the most herbivorous lineages (Pérez-Mellado & Traveset, 1999 and references therein; Pérez-Mellado *et al.*, 2000a, b; Nogales *et al.*, 2002; Riera *et al.*, 2002).

All these facts strongly suggest that herbivory in lacertids, even though partial, is a true specialisation in morphological and behavioural terms. However, evolutionary history becomes fundamental for explaining distribution of this phenomenon across species. Examining parasite fauna Roca (1999) proposed for a carnivorous-herbivorous continuum in reptiles. Independently of the environmental pressures favouring plant consumption (insular conditions), evolutionary time under such pressures is needed to develop behavioural, physiological and morphological specializations along this continuum (Carretero *et al.*, 2001). Three lineages taken as old colonisers of islands free from terrestrial predators, *Gallotia* in Canary Islands (12.6 mya, Carranza, 2002), *Podarcis* in the Balearics (7-5 mya, Alcover *et al.*, 1981) and *Lacerta (Teira) dugesii* in Madeira (2.8 mya, Brehm *et al.*, 2003), all show adaptations to herbivory. The most ancient lineage is the most herbivorous and shows the deepest modifications although not nearly as those shown by other more basal lineages such as Iguanidae *sensu stricto* (King, 1996).
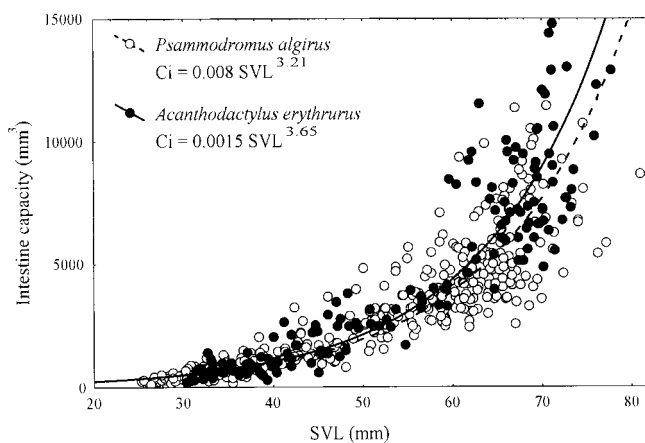

Fig. 4 - Positive allometry between intestine and body size in two lacertid species (Carretero 1997). Within species, juveniles have smaller intestines than adults. Between species, *Acanthodactylus erythrurus* shows higher intestine capacity than *Psammodromus algirus*.

MIRMECOPHAGY AND OTHER SPECIALISATIONS

Even if herbivory is excluded, it is clear that not all lacertids in the Mediterranean are food generalists. *Acanthodactylus*, *Mesalina*, some members of *Podarcis* and even *Psammodromus* have highly mirmecophagous diets (Carretero & Llorente, 1991, 2001; Pérez-Mellado, 1992; Pérez-Mellado & Corti, 1993). This phenomenon is not uncommon in the family since other members outside the region are also ant specialists (*Meroles*: Branch, 1988), whereas others have diets based on termites (*Nucras*, *Ichnotropis*, *Pedioplanis*: Pianka, 1986; Branch, 1988; Spawls *et al.*, 2002) or even scorpions (*Nucras*: Pianka, 1986; Branch, 1988). Of the European species, which are the best studied, *A. erythrurus* consumed ants in great numbers (70-80% of diet) at sites where other lacertids did not and showed positive selection for them (Pollo & Pérez-Mellado, 1988; Gil *et al.*, 1993); *P. hispanicus* also selected ants but consumed them less frequently (15-20%: Pollo & Pérez-Mellado, 1988; Carretero & Llorente 1991). The first species is the only European representative of a lineage ranging from North Africa to South-west Asia and inhabiting arid areas (Harris & Arnold, 2000) where ants are probably the main prey available. It has been argued that mirmecophagy evolved under such conditions involving a change in foraging strategy and then became fixed when this species reached more mesic areas in Europe (Gil *et al.*, 1993). Nevertheless, such specialisation does not seem absolute since ants in diet decreased (10-20%) and were replaced by other prey at the species' northern boundary (Carretero M. A., 1993, Ph.D. Thesis, University of Barcelona; Carretero & Llorente, 1993).

The foraging shift to clumped prey hypothesised by Gil *et al.* (1993) for *A. erythrurus* (see also Belliure *et al.*, 1996) could also be applied to other species, especially insular *Podarcis* (Pérez-Mellado & Corti, 1993; Carretero & Llorente, 2001). In poor environments, this strategy may minimise prey search costs which could compensate for the low energy intake per prey item (Gil *et al.*, 1993; Pérez-Mellado & Corti, 1993). The consumption of ants (and social Aphididae) by Balearic *Podarcis* increased in parallel with plant matter in summer, which suggests similar selective pressures (Pérez-Mellado & Corti, 1993; Carretero & Llorente, 2001). Ant-eating in lizards usually involves physiological adaptations for detoxification (Schmidt *et al.*, 1989) and morphological changes such as a bigger gut for digesting a prey with low profitability (Pianka, 1986). In fact, *A. erythrurus* showed greater digestive capacities than other Mediterranean lacertids (Carretero, 1997) but the same kind of analysis performed with plant matter failed to detect any correlation between ant consumption and gut size (Carretero M. A. *et al.*, 1999, *Abstract* in X Meeting S.E.H., Irakleio, Greece, pp. 41-42) (Fig. 5).

DIET SAMPLING

All the above is based on the assumption that lacertid diet can be reliably assessed. However, as not all sources of diet are equivalent, it is important to be aware of the pros and cons of different methods (Table I) to be applied in different situations.

Despite its non-invasiveness, direct observation is less useful in lacertids than in other vertebrates because predation is not observed often enough to provide a big enough sample and observations are strongly biased towards open areas. Nevertheless, focal observations are worthwhile in order to analyse repeated individual behaviours and foraging mode (Perry *et al.*, 1990; Belliure *et al.*, 1996). Stomach flushing has been used in lacertids (Richard & Lapini, 1993; Bombi & Bologna, 2002), but results are less positive that in amphibians (Joly, 1988) due to the anatomy of their oesophagus which is very narrow and causes difficulties when preys are pumped out (personal observations). Because of this, the technique is only partially non-invasive (some individuals are damaged) and diet information is biased (small prey are extracted easier than big ones). Analysis of faecal pellets is a non-invasive technique recommended for studying species or populations with conservation problems (see for instance Pérez-Mellado *et al.*, 1999). Pellets are easy to find and can be collected in great amounts with replication. Nevertheless, this method suffers from some drawbacks: individual, class

TABLE I - *Comparative traits of the different methods used for assessing diet composition and prey availability in lacertids. Y, yes; N, no.*

Diet

Method	Sample	Invasive	Bias	Replication
Direct observation	limited	N	Y	Y
Stomach flushing	medium	Y/N	Y	Y/N
Faecal pellets	large	Y	Y	Y
Gut contents (stomach/intestine)	large	Y	N/Y	N

Availability

Method	Effort	Selection	Secondary loss	Time control	Area control
Pit-fall traps	passive	terrestrial prey	Y	N	N
Adhesive traps	passive	moving prey	Y/N	N	N
Netting	active	probable	N	Y	N
Biocenometers	active	N	N	Y	Y

and even species assignation is doubtful except if lizards are captured and forced to defecate; pellets are not randomly deposited (i.e., in the most prominent sites and by the dominant individuals, López et al., 1998) and prey composition is seriously biased (see below). Finally, gut content examination is the most common method. However, this involves sacrificing lizards, which prevents replication and means it cannot be practised on endangered species. The bias information depends on the digestive segment analysed. Carretero & Llorente (2001) compared diet analysed in stomach and intestine from the same individual in a population of *P. hispanicus* (see Fig. 6). Their conclusions were that prey representation in the intestine was impoverished (lower diversity if sample size < 40) and seriously biased towards hard and big items. These Authors recommended not mixing results coming from different gut compartments, to make homogeneous comparisons and always exclude the rectum (which is equivalent to pellets in composition).

Similarly, studies of prey selection also rely on assessment of trophic availability. As for diet information, different methods have been used with varying reliability (Southwood, 1976; Table I). Passive methods have been intensively used because they involve less field time, which can then be devoted to collecting information on lizards (Díaz, 1995). However, passive methods involve any kind of selection and do not control for time or area sampled. Pit-fall traps are only adequate for estimating abundance of terrestrial prey on the ground but do not collect either flying or climbing prey (Heulin, 1985). Adhesive traps show some advantages since they can be stuck to vertical surfaces and collect flying prey, whilst still selecting for moving prey (Heulin, 1985). Netting is an active method which is useful in bushy

habitats and allows control of time effort. However, lack of selection is not guaranteed and the area surveyed is unclear. The biocenometer consists of a portable net cube (usually 1×1×1 m) fixed to the ground, from which the researcher collects all prey present with a portable vacuum cleaner (Llorente et al., 1999). The advantages of this method are that all prey types are sampled equally in a defined area (or volume) and during a restricted time interval. This allows the modelling of prey production in a study plot and exploration of relationships with lizard density. Obvious limitations are the effort involved and the impossibility of application in certain habitats (steep, rocky). Specific methods must be used for evaluating plant availability in herbivorous species (Orrit et al., 1999).

DESCRIPTORS AND DIVERSITY

The way diet is described is not irrelevant since poor analysis can limit further interpretation. The paragraphs below contain some methodological remarks that could improve the diet analysis of lacertids. Examples of application of this methodology to lacertids can be found in Carretero & Llorente (1991, 1993, 2001), and Carretero et al. (2001).

When analysing stomach contents, the proportion of empty stomachs (repletion index) should first be quantified. This parameter is highly valuable in diet analysis at seasonal and species levels (Carretero & Llorente, 2001; Huey et al., 2001). At the population level, the traditional way of presenting diet results relies on two indices: occurrence (%P) and abundance (%N). Although only the second is usually taken into account, both have ecological relevance (Fig. 7). The first de-
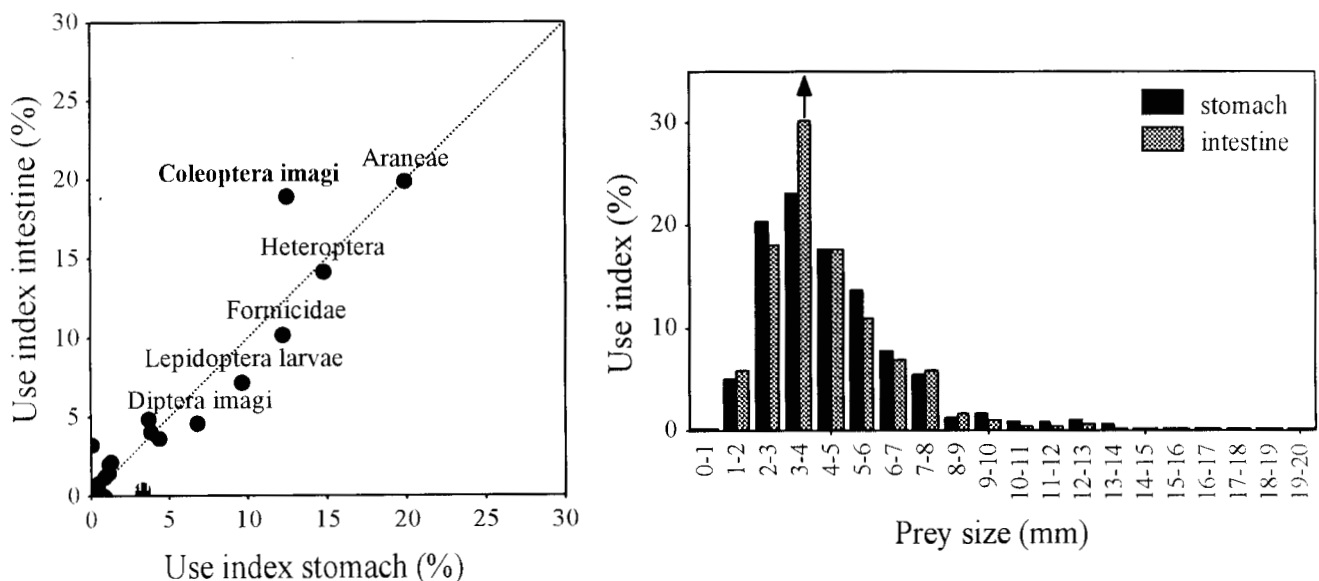

Fig. 6 - Comparative analysis of taxa and prey size between stomach and intestine in *Psammodromus hispanicus* (Carretero & Llorente, 2001). Hard, big preys are over-represented in the intestine.

scribes the 'horizontal' distribution among individuals, whereas the second describes the 'vertical' distribution of various prey classified as OTUs (Operational Taxonimc Units, Sneath & Sokal, 1973). Nevertheless, this description is unsatisfactory since no overall idea of prey importance is provided. To solve this problem, several hybrid approaches were developed (see Costello, 1990; Amudsen *et al.*, 1996). One of these was the probabilistic index (IP or λ'' of Ruiz X. & Jover L., 1981, *Abstract* in XV Congr. Int. Fauna Cinegética y Silvestre. Trujillo, Spain), defined as the probability of repetition in the trophic matrix (individuals × OTUs) (Fig. 7). However, this procedure still ignored differences in homogeneity of 'horizontal' distribution and tended to over-represent 'oligo-elements'. Because of this, it was replaced by the resource use index (IU, Jover L., 1989, Ph.D. Thesis, University of Barcelona) which is a combination of numerical abundance and a 'horizontal' diversity index (Fig. 7). The same procedure can also be applied to prey sizes and biomasses (Roig J. M. *et al.*, 1998, *Abstract* in III Int. Symp. Lacertids of Mediterranean Basin. Cres, Croatia: 70). Table II compares of all four indices in a case example.

Another important descriptive parameter is trophic diversity, which can be split into two components: the number of OTUs and evenness or equitability (Magurran, 1988). It should be noted that variation either in OTU number or in uniformity of different OTUs can produce changes in diversity. Margalef's index (or Brillouin's index for diet) $I_{Mg} = (\frac{1}{N})$ (log$_2$ N!-Σ log$_2$ Ni!) is more correct for diet analysis than are other diversity indices (Hurtubia, 1973; Pielou, 1975) but was used less in the past precisely because of difficulties in calculation. Following Jover L. (1989, Ph.D. Thesis, University of Barcelona) three different types of diversity could be calculated (Fig. 8; see Magurran, 1988, for a different
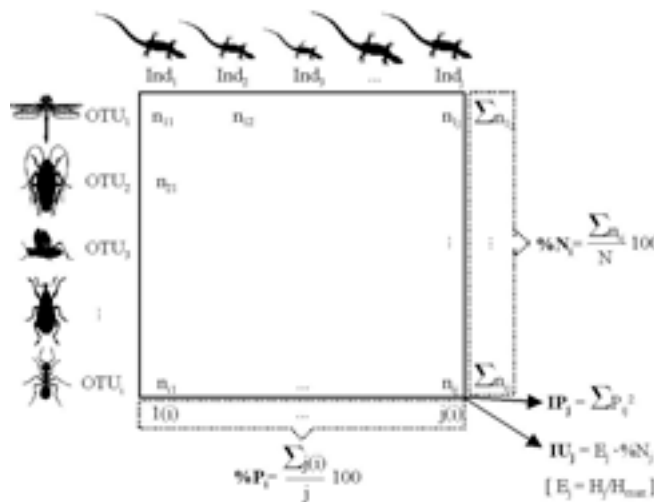

Fig. 7 - Diagram explaining the calculation procedures of four diet descriptors. T, total number of prey; %P, percentage of occurrence; %N, percentage of abundance; IP, probabilistic index (λ''); IU, resource use index.

TABLE II - *Comparative results of four descriptors of the taxonomical diet of* Psammodromus hispanicus *based on 211 stomach contents (Carretero & Llorente, 1991). T, total number of prey; %P, percentage of occurrence; %N, percentage of abundance; IP, probabilistic index (λ''); IU, resource use index.*

OTU	T	%P	%N	IP	IU
Stylommatophora	2	0.47	0.19	0.16	0.00
Isopoda	45	10.43	4.18	4.33	3.23
Pseudoescorpiones	13	5.21	1.21	0.68	0.79
Opiliones	16	6.16	1.49	1.77	1.09
Araneae	168	48.82	15.61	16.85	19.87
Acarina	5	1.90	0.47	0.49	0.18
Lithobiomorpha	2	0.95	0.19	0.07	0.04
Microcoryphia	14	5.69	1.30	0.90	0.88
Dictyoptera	17	7.11	1.58	1.69	1.23
Orthoptera	45	18.01	4.18	5.27	4.32
Dermaptera	2	0.95	0.19	0.28	0.04
Neuroptera larvae	7	3.32	0.65	0.37	0.38
Lepidoptera larvae	85	31.75	7.90	8.39	9.54
Lepidoptera imagines	16	6.64	1.49	1.72	1.13
Diptera larvae	9	2.84	0.84	0.58	0.34
Diptera imagines	69	22.27	6.41	6.10	6.72
Coleoptera larvae	36	13.74	3.35	1.86	3.20
Coleoptera imagines	115	36.49	10.69	11.47	12.41
Hymenoptera (no Form.)	60	16.59	5.58	5.52	3.70
Formicidae	142	24.64	13.20	12.34	12.22
Homoptera	49	15.64	4.55	3.43	3.84
Heteroptera	153	34.12	14.22	14.29	14.77
Ova insecta	5	1.42	0.47	0.46	0.11
Insecta indet.	1	0.47	0.09	1.00	0.00

approach). Total accumulated diversity (Hn) of the whole sample is not very informative, since it lacks variation and depends on sample size. Mean individual diversity (Hi) provides central and dispersal statistics at an individual level. Population diversity (Hp), defined as the total accumulated diversity of an infinite sample, can be estimated from a real sample by pseudosampling methods such as Jack-knife (Jover L., 1989, Ph.D. Thesis, University of Barcelona). Unlike Hn, both Hi and Hp admit statistic inference for group comparisons and the degree of interindividual variation can be analysed within the same group.

PERSPECTIVES

From the beginning of optimal foraging theory, lizards have been used as model organisms (Pianka, 1966). Although initial models of lacertid trophic ecology were simple (essentially, lizard + arthropod availability + anatomical constraints), they have gradually been turning into complex pictures due to the incorporation of an increasing number of factors (Fig. 9), some of them still virtually unexplored.

The studies mentioned above indicate that some lacertid species assess certain prey traits such as size, han-
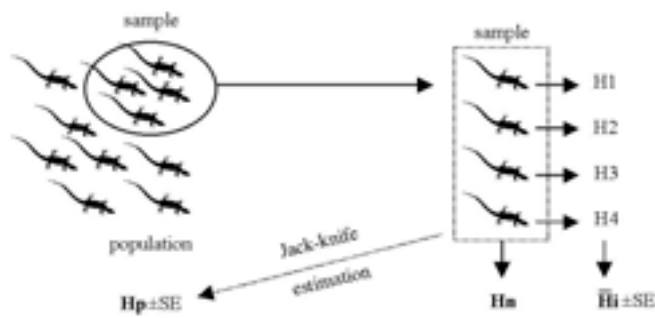
Fig. 8 - Diagram explaining the calculation procedures for three types of diversity. Hn, total accumulated diversity; Hi, mean individual diversity; Hp, population diversity estimated by Jack-knife.

dling time, energy and nutrients. Other factors, however, may also be involved. For instance, prey water content, and environmental humidity may modify foraging activity, especially in those species living in arid environments (Bowker, 1993; Rocha, 2000). Few studies have considered mobility and defensive behaviour of prey (Wehner et al., 1992), which seriously limit the application of foraging theory (Sih & Christensen, 2001). Analyses of prey spatial distribution (Pitt & Ritchie, 2002) are also lacking, though they could be useful for elucidating the environmental constraints of different foraging strategies. Such studies should be combined with quantitative recording of foraging behaviour in the field (Perry, 1990; Belliure et al., 1996) and not mere classification of species into sit-and-wait (apparently not appearing in Mediterranean lacertids) and active foragers (Huey & Pianka, 1981).

To move on to factors not directly related with prey, there is enough evidence to accept the influence of predation risk, although more mechanistic behavioural studies (Cooper, 2000) should be carried out. Virtually nothing is known about the influence of parasites on foraging, but correlation between helminthofauna and herbivory has been reported (see Roca, 1999; Roca et al., manuscript submitted). Until now, foraging has been considered in isolation but this seems unrealistic for dense populations and complex communities of Mediterranean lacertids. Though not very popular in the last decade, competitive interactions, both inter- and intraspecific, should not be ignored in foraging studies (Carretero & Llorente, 1993). Interference between species, already demonstrated in lacertids (Bauwens & Downes, 2002), should have trophic consequences. More costly demonstration of exploitative competition would require quantification of trophic availability (by means of biocenometers), modelisation taking into account lizard densities and metabolic rates (Brown et al., 1992; Brown & Pérez-Mellado, 1994) and, eventually, evaluation of its effects in situ (Ballinger, 1977). Only more accurate estimation of the body and reproductive condition of lizards could account for the proximate

causes of seasonal changes in foraging tactics. For instance, in the tail removal experiments, it is difficult to discriminate between the effects of increased predator vulnerability and metabolic changes derived from reserve loss and regeneration.

Many published results should be reinterpreted in the light of the learning capacities shown by lacertids (Desfilis & Font, 2002). In essence, these imply that consecutive foraging acts are not independent. If true, this would affect ontogenic and seasonal variation in diet. Even the possibility of selection of this trait should be considered.

Finally, these complex but more realistic models of optimality should be tested against alternative, non-adaptationist hypotheses (Perry & Pianka, 1999). Some traits observed could be just exaptations, functionally related with foraging but originating secondarily from selective pressures on other traits (i.e., reproduction: Pianka, 1986; Arnold, 1993). At present, preliminary evidence supports in some cases the influence of evolutionary history on foraging tactics (see above). Nevertheless, comparative studies on enlarged data sets of species should be carried out in order to quantify phylogenetic influence on foraging behaviour. Consequently, some of the results already obtained for one species or lineage could be not generalisable to others.

In the mid sixties, lacertids were thought to be workers eating resignedly the set menu in the factory restaurant. Over almost forty years, it has become more and more evident that they can ask for some dishes a la carte and even choose another restaurant. To interpret the reasons and constraints for such choices and the constraints on them is the main task of trophic ecologists in the near future.
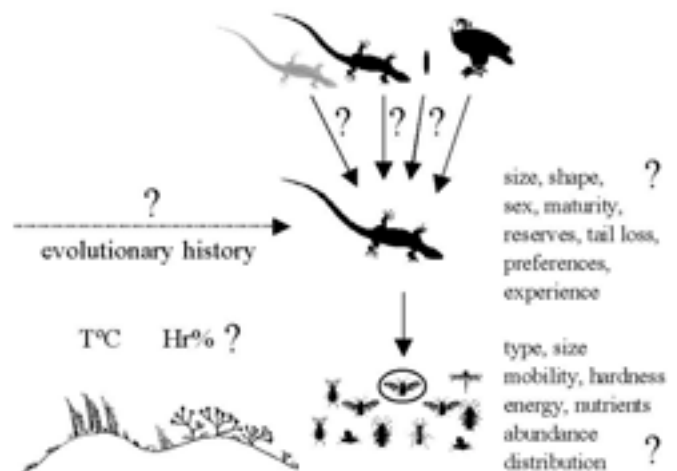

Fig. 9 - Diagram representing different factors involved in trophic ecology of lacertids. Question marks point out unexplored aspects.

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