Diet Composition of the Lizard *Lacerta lepida* in Central Spain

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ABSTRACT.-We studied diet composition of *Lacerta lepida* in a sample of 325 specimens from central Spain. This large lacertid lizard feeds predominantly on Coleoptera, but also consumes other arthropods, snails, small vertebrates, and some plant material. Composition of the animal fraction of the diet and trophic diversity were virtually identical in adult males and females. Juveniles fed upon a restricted number of prey types which were small in size, whereas adults consumed a large number of prey taxa, covering a wider range of prey sizes. Trophic segregation among individual lizards was highest in the smaller size classes. The incidence of plant material increased with lizard size and was highest in males, but it never represented a substantial fraction of the total diet. The contribution of small vertebrates to total prey numbers also increased with lizard body size. Our results indicate that vertebrates are of marginal numerical importance to the diet of *L. lepida*.

Most lizards feed primarily on arthropods, although some species have adopted a diet consisting mainly of molluscs, plant material or small vertebrates (see Greene, 1982). Insectivorous lizards are often opportunistic feeders, eating any suitable sized arthropods. Hence, diet composition has been shown to exhibit seasonal or (micro)geographic variation, in response to a shift in prey availability which is either presumed (e.g., Avery, 1966; Mou and Barbault, 1986; Arnold, 1987) or documented (e.g., Ballinger and Ballinger, 1979; Stamps et al., 1981; Mou, 1987). Body size is another factor that influences prey choice and diet composition (Pough, 1973). Although most evidence for a relation between body size and dietary composition derives from interspecific comparisons, ontogenetic changes in prey choice within single lizard species have been described (see Pough, 1973; Greene, 1982).

European lizards of the family Lacertidae are basically insectivorous, although some forms occasionally eat other invertebrates, small vertebrates or plants (see Arnold, 1987). *Lacerta lepida*, the largest European lacertid (adult snout-vent-length 140-220 mm), is a diurnal, heliothermic, ground-dwelling lizard that is found in a variety of mediterranean habitats throughout most of Spain and Portugal, in southern...
France and extreme northwest Italy. Diet composition, one of the best studied features of the biology of this lizard, has been treated by a large number of authors (Peters, 1962; Valverde, 1967; Mellado et al., 1975; Escárce and Veriead, 1981; Pérez-Mellado, 1981; Bas, 1982; Seva, 1982; Bischoff et al., 1984; Brana, 1984; Mateo, 1988; and Busack and Visnaw, 1989). However, most studies were based on small samples, and made no distinction between lizard sex or size classes.

*Lacerta lepida* experiences a >100-fold increase in body mass during its ontogeny (from 2 to 280 g), and the sexes differ notably in maximum body size and head dimensions (Castilla, 1989). We hypothesized that such morphological differences might induce diverging prey choices. One of the most controversial aspects of this lizard’s feeding ecology is the common belief that it preys extensively on small vertebrates, particularly eggs and chicks of the Red-legged Partridge (*Alectoris rufa*), an important game bird in Spain. Although published studies do not support this opinion, one could argue that the dietary contribution of vertebrate prey might have been underestimated due to the examination of small numbers of lizards from restricted areas.

We here report diet composition in populations of *L. lepida* from central Spain. Our major objectives were: (1) to provide quantitative information on the types and sizes of prey; (2) to analyse diet composition and trophic diversity in distinct lizard size/sex classes; (3) to examine the incidence of herbivory in relation to lizard size; and (4) to provide quantitative data on the consumption of vertebrates, using a large sample of lizards from different localities, including one where partridges are particularly abundant.

**MATERIAL AND METHODS**

*Study Area and General Procedures.*—We used museum specimens to sample a range of localities, seasons and lizard size/sex groups. Lizards were obtained from the collections of the "Unidad de Zoología Aplicada" (Madrid, Spain). Specimens had been collected during the period 1972-1982 at different sites within the central Spanish provinces Cáceres, Toledo, and Ciudad Real (geographical limits: 40°30'N/7°35'W to 38°20'N / 2°35'W), at altitudes ranging from 290 to 908 m. A subset (95 adult lizards) of the total sample was collected specifically for this study within a restricted hunting field (Sta. Cruz de Mudela, prov. Ciudad Real) with exceptionally high partridge densities due to game-management practices. Rivas-Martinez (1982) provides information on the climate and vegetation in central Spain.

We examined a total of 325 preserved lizards. Snout-vent length (SVL) was measured and contents of the digestive tract were removed. We recorded presence of mineral and vegetable material; the latter was identified to the taxonomic order of family. Animal prey items were identified at least to order. We measured the length of (nearly) intact prey that were encountered in the stomachs of 204 lizards and calculated mean lengths of measurable prey in each stomach as an estimate of prey sizes consumed by that lizard.

We grouped lizards according to sex (relative head size and gonads; see Castilla, 1989), size (‘=age) class (juvenile: ≥7:0 mm SVL, mass = 2-8 g; subadult: 71-139 mm SVL, mass = 10-80 g; adult: 140 mm SVL, mass = 80-280 g), and season (spring: March-May; summer: June-August; autumn: September-October). We included all lizards in the overall description and analysis of diet composition; the analyses of sexual and seasonal variation in diet composition are based on the stomach contents of adult lizards, for which sample sizes were largest.

*Mathematical Procedures.*—We quantified the numerical contribution of a prey type to diet as the percentage of total prey numbers that corresponded to that prey type. Trophic (food taxonomy) diversity was estimated with Brillouin’s diversity index:

\[
H = \frac{1}{ln} \times (\log n! - \log n!) 
\]

where \(n\) is the total number of prey items and \(n\) the number of prey items belonging to a given taxonomic category. To facilitate interpretation of differing diversity values, we also calculated the number of prey groups eaten, and an index of evenness:

\[
J = \frac{H}{H_{max}}
\]

where \(H\) is the calculated diversity, and \(H_{max}\) the maximal diversity that could possibly be found in the sample (see Pielou [1969, 1975] and Magurran [1988] for details of computation).

Trophic diversity was estimated both at the individual and population level. Individual diversity (\(H_{ind}\)); prey taxon diversity, evenness, and the number of prey categories were calculated for each individual lizard. The average values and their 95% confidence intervals were calculated using all individuals belonging to the lizard group (sex, length class, season) considered. Population diversity (\(H_{pop}\)) was calculated following procedures outlined in Pielou (1969, 1975). Briefly, the method consists of ordering the different stomachs in a random sequence and adding them to the collection one at a time. The cumulative diversity for the collection is computed after adding each stomach, and its value is plotted against the number of incorporated stomachs. This curve flattens off after including a number of individuals that is
sufficiently large as to obtain a representative coverage of the population. The flattened portion of the curve is then used to calculate H_{pop} and its 95% confidence interval (see Pielou, 1975 for details). As the estimate of H_{pop} for a given data set is based on a random ordering of individual stomachs, each random sequence will produce a different estimate. We followed recommendations of Lloyd et al. (1968) and calculated 10 estimates of H_{pop} for each data set, and selected the median value as the best estimate of population diversity.

The statistical significance of differences between diversity or evenness estimates were assessed by their non-overlapping confidence intervals (a = 0.05).

Food overlap values between lizard groups j and k were calculated with Pianka's (1973) symmetric index:

$$O_{jk} = \frac{\sum \min(p_{ij}, p_{kj})}{\sqrt{\sum p_{ij}^2 \cdot \sum p_{kj}^2}}$$

where p_{ij} and p_{kj} are the proportions of prey category i in the diet of lizard groups j and k, respectively.

We estimated food overlap between individuals within the same lizard group by calculating overlap values between all possible pairs of individual lizards. These values were then averaged and the 95% confidence interval of the mean was computed. Estimates of food overlap between lizard groups were based on the pooled stomach contents of all individuals from each group.

We used Kruskal-Wallis analyses of variance to compare lengths of prey consumed by different lizard groups, and Spearman rank correlations to assess covariance between prey length and lizard size (SVL).

RESULTS

Taxonomie Composition of the Diet.-Only 5 of 325 lizards examined had no remnants of food material in their digestive tracts. We identified a total of 9600 prey items (9542 invertebrates and 58 vertebrates) that belonged to 20 invertebrate and 7 vertebrate orders.

The following vertebrate species were identified: Crocidura sp., Mus sp., Apodemus sylvaticus, Microtus duodecimcostatus, Elymus quercinus, Alectoris rufa, Lacerta lepida, Podarcis hispanica, Psammomodonus algirus, Psammomodonus sp., Blanus cinereus, Natrix sp., and Pelobates cultripes. We recorded remains of both chicks and eggs of Red-legged Partridge (Alectoris rufa). Predation on partridges was highest in the hunting field, where their remnants represented 0.71% (22/3112) of the total prey numbers. In the remainder of the sample, this game bird represented 0.25% of all prey.

Coleoptera were the most important prey group, followed by Hymenoptera, Lepidoptera, Orthoptera and Heteroptera. All other prey taxa were encountered only sporadically (<1% of total prey numbers; Table 1).

Within the Coleoptera, species of the family Scarabaeidae were numerically most important (60% of total number of Coleoptera), followed by Chrysomelidae, Tenebrionidae, and Curculionidae. Representatives of 14 other beetle families were encountered in low numbers (<4% of total). Most Hymenoptera eaten were members of the genera Apis and Vespa; we detected ants rarely.

The mean number of prey counted per stomach ranged from 8.9 in juveniles to 35.0 in adults. Exceptionally large numbers of prey items were encountered in some adult lizards (>200 prey in 3 lizards; 100-199 prey in 11 stomachs), and were always the Scarabid beetle Chasmatopterus villosulus.

Diet similarity among lizard size classes was high, as illustrated by the high food overlap estimates (juveniles-subadults: O = 0.974; juveniles-adults: O = 0.986; subadults-adults: O = 0.936). The most notable differences were an increase in the relative abundance of Coleoptera, Lepidoptera, and vertebrates with lizard size. The contribution of Hymenoptera and, to a lesser extent, of Araneida and Orthoptera decreased with lizard size (Table 1). Diets of adult males and females were virtually identical (O = 1.000). The composition of the adults' diet was highly similar in spring and summer (O = 0.998). Food overlap estimates were much lower between spring-autumn (O = 0.457) or summer-autumn (O = 0.504). During autumn, the diet consisted almost exclusively of Orthoptera and Coleoptera (Table 1).

Trophic Diversity.- Mean individual prey taxon diversity increased with lizard size (Table 2). Comparisons of the confidence intervals indicated a significant difference between juveniles and adults. As evenness estimates remained approximately constant across size classes, the increase in individual diversity seems primarily a consequence of an increment in the number of prey taxa eaten (Table 2). Food overlap values between individuals in each size class were highest in the adults. Population diversity estimates did not differ significantly among lizard size classes, although evenness decreased and the number of prey types consumed increased significantly with lizard size (Table 2).

Both individual and population diversity, together with their associated evenness estimates, had similar values in adult males and females.
(Table 2). Individual diversity estimates were lowest during autumn, mainly as a consequence of the low number of prey taxa eaten. We found no seasonal differences in the interindividual overlap values. Population diversity and the number of prey taxa were lowest, whereas population evenness was highest during autumn (Table 2).

**Prey Size.** Prey size differed markedly among lizard size classes (Kruskal-Wallis: H = 24.1, 2 df, P < 0.001). Both average prey length and the range of prey sizes consumed were largest

| **TABLE 2.** Estimates (mean ± 95% confidence limits) of individual diversity (H,nd), evenness O,nd), number of prey taxa consumed (C,nd), interindividual overlap (O,nd), and population diversity (Hpop; estimate ± 95% confidence limits), population evenness (Hpop), and the number of prey taxa eaten (Cpop) for different categories of lizards. N = numbers of individual lizards. |
|---|---|---|---|---|---|---|---|---|---|
| **N** | **H,nd** | **Jind** | **eind** | **Uind** | **H^0.95** | **Cpop** | **O,nd** |
| **Juveniles** | 32 | 0.505 ± 0.168 | 0.324 ± 0.109 | 2.1 ± 0.4 | 0.500 ± 0.05 | 2.098 ± 0.468 | 0.684 | 9 |
| **Subadults** | 40 | 0.757 ± 0.130 | 0.413 ± 0.092 | 3.0 ± 0.4 | 0.563 ± 0.045 | 2.376 ± 0.590 | 0.608 | 16 |
| **Adults** | 248 | 0.875 ± 0.061 | 0.309 ± 0.026 | 3.9 ± 0.2 | 0.699 ± 0.008 | 2.088 ± 0.207 | 0.436 | 28 |
| **Males** | 157 | 0.839 ± 0.080 | 0.303 ± 0.033 | 3.7 ± 0.2 | 0.693 ± 0.014 | 2.072 ± 0.268 | 0.438 | 27 |
| **Females** | 91 | 0.935 ± 0.097 | 0.319 ± 0.043 | 4.2 ± 0.4 | 0.708 ± 0.024 | 2.090 ± 0.294 | 0.479 | 21 |
| **Spring** | 110 | 0.815 ± 0.092 | 0.280 ± 0.038 | 4.0 ± 0.3 | 0.732 ± 0.020 | 1.938 ± 0.361 | 0.425 | 24 |
| **Summer** | 131 | 0.949 ± 0.084 | 0.337 ± 0.036 | 4.0 ± 0.3 | 0.703 ± 0.016 | 2.065 ± 0.294 | 0.447 | 25 |
| **Autumn** | 7 | 0.410 ± 0.403 | 0.245 ± 0.237 | 1.7 ± 0.7 | 0.734 ± 0.370 | 0.979 ± 0.312 | 0.685 | 3 |
### Table 3. Snout-vent lengths and lengths or prey eaten in distinct size/sex classes of *Lacerta lepida*. N = number of lizards.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>SVL (mm)</th>
<th>Prey length (mm)</th>
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<tr>
<td></td>
<td></td>
<td>i ± 1 SD</td>
<td>Range</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>23</td>
<td>62.9 ± 6.8</td>
<td>43-70</td>
</tr>
<tr>
<td>Subadults</td>
<td>13</td>
<td>113.9 ± 28.0</td>
<td>73-135</td>
</tr>
<tr>
<td>Adults</td>
<td>83</td>
<td>189.1 ± 23.2</td>
<td>140-230</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juveniles</td>
<td>10</td>
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<td>54-66</td>
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<tr>
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</tr>
<tr>
<td>Adults</td>
<td>64</td>
<td>169.1 ± 17.7</td>
<td>140-200</td>
</tr>
<tr>
<td>Total</td>
<td>204</td>
<td>114.4 ± 51.5</td>
<td>43-230</td>
</tr>
</tbody>
</table>

in the adults (Table 3). Comparisons of prey lengths for males and females separately showed a significant difference among lizard size classes in the males (Kruskal-Wallis, $H = 18.33, 2$ df, $P < 0.001$), but not in females (Kruskal-Wallis: $H = 5.32, 2$ df, $P > 0.05$; Table 3).

We found significant correlations between mean prey size and lizard SVL in both males ($r = 0.443, N = 119, P < 0.001$) and females ($r = 0.281, N = 85, P < 0.001$).

Presence of Plants and Minerals.- Remnants of plants were encountered in $80\%$ ($N = 255$) of the stomachs that contained any food. The incidence of plant remains was highest in males (males: $86\%, N = 175$; females: $68\%, N = 80$; $G = 13.070, 1$ df, $P < 0.001$) and increased significantly with lizard size (juveniles: $44\%, N = 14$; subadults: $35\%, N = 14$; adults: $92\%, N = 227$; $G = 79.561, 2$ df, $P < 0.001$).

Plant remains encountered corresponded to the following families: Gramineae (seeds, blades and stalk fragments); Fabaceae (fragments and intact leaves of *Quercus rotundifolia* and *Q. cocci/era*); Vitaceae (intact grapes and their seeds); Cistaceae (leaves of *Cistus sp.*); Compositae (fruits and a flower of *Calendula sp.*); Leguminosae (stalks and fruits of various species, fruits of *Medicago sp.*); Anacardiaceae (leaves of *Pistacia lentiscus*); Ericaceae (leaves of *Arctostaphylos uva-ursi*); Rosaceae (fruits of *Rosa sp.* and *Rubus sp.*); Umbelliferae; Cupressaceae; Labiatae; and Jun- caceae (fruits, seeds and leaves).

We also encountered fragments of plastic, paper, and stones in the lizards’ stomachs. Mineral material included slate, quartz, quartzite, granite, day, and sand. Stones were encountered in $23\%$ ($N = 73$) of all stomachs. The number of stones per digestive tract varied between 1 and 12; the largest had a diameter of 10 mm. The proportion of stomachs containing mineral material did not differ between sexes (males: $21\%, N = 42$; females: $26\%, N = 31$; $G = 1.097, 1$ df, $P > 0.20$) or lizard size classes (juveniles: $28\%, N = 9$; subadults: $18\%, N = 7$; adults: $23\%, N = 57$; $G = 1.148, 2$ df, $P > 0.30$).

**DISCUSSION**

In central Spain, *L. lepida* preys predominantly on Coleoptera, but also consumes a wide variety of other arthropods, snails, small vertebrates, and plant materials. The wide array of prey taken and the occasional mass consumption of presumably aggregated individuals of a single prey species suggest opportunistic feeding habits. The numerical predominance of Coleoptera has also been reported in other parts of this lizard’s range (Peters, 1962; Valverde, 1967; Mellado et al., 1975; Escarré and Vericad, 1981; Pérez-Mellado, 1981; Bas, 1982; Seva, 1982; Bischoff et al., 1984; Braii.a, 1984; Mateo, 1988; and Busack and Visnaw, 1989). In the absence of estimates of prey availability, it remains unclear whether lizards actually exhibit a preference for Coleoptera or take different prey proportional to their relative abundance in the environment.

Gastropoda were virtually absent from the lizards’ diet in central Spain, but were numerically important (25-40% of total prey number) at several other regions (Pyrenees, Peters [1962]; Galicia, Mateo [1988]; and Alicante, Valverde [1967], Escarré and Vericad [1981], Mateo [1988]). These regions are all characterized by relatively high levels of precipitation and a supposed great abundance of snails. Some authors have reported the occasional importance (20% of prey numbers) of some insect orders such as Orthoptera (Peters, 1962), Lepidoptera (Valverde, 1967; Braii.a, 1984) and Hymenoptera (Pérez-Mellado, 1981; Mateo, 1988). Mateo (1988) described the exceptional situation of an insular population (Isla de la Paloma) where vegetable material makes up the bulk of the diet. These findings highlight the flexibility of feeding habits and diet composition in *L. lepida*.

The consumption of small vertebrates is an
of ten documented aspect of this lizard’s feeding ecology (Peters, 1962; Salvador, 1974; Bischoff et al., 1984) and has even been exaggerated, referring to the great voracity of this species in captivity (Hofmann, 1963; Siegel, 1963). Our results, together with those of previous studies, indicate clearly that vertebrates are of marginal numerical importance in the diet of *L. lepida*. Predation on chicks and eggs of *A. rufa* has been documented by occasional findings or observations (Mellado et al., 1975; Calderón, 1977; De Juana and De Juana, 1982), and this has resulted in the removal of lizards during game management activities. However, quantitative data reported here do not support the common belief that *L. lepida* has an important impact on partridge populations.

A surprisingly high proportion (80%) of the lizards examined contained plant material, but this never represented a substantial fraction of the food volume. Plant material should hence be considered as additional food in a basically insectivorous diet. It should be noted that adult *L. lepida* attain the body mass that is associated with a shift from carnivory to herbivory in the lizard families Iguanidae, Agamidae and Scincidae (100-300 g; Pough, 1973). The incidence of vegetable material increased with lizard size and was highest in males, which attain larger lengths and weights than the females (Castilla, 1989). Such size-related shifts in the degree of herbivory have previously been described many times (see Pough, 1973; Greene, 1982).

We found few differences between lizard size/sex groups in dietary composition. The virtually identical composition of the diet in males and females, as well as the similarity of the trophic diversity estimates, suggests that the sexes have similar foraging habits and prey chokes, despite differences in morphometric characters (body size, relative head dimensions) that may influence feeding ecology. Lizard size groups exhibited high resemblance with respect to the taxonomic composition of their diet. However, the study of trophic diversity revealed some differences in feeding habits among the size classes. At the individual level, the mean number of prey taxa, but not evenness, increased with lizard size, resulting in a parallel increase in average individual diversity. Interindividual overlap values were lowest in juveniles and subadults, indicating a higher degree of trophic segregation among individuals of these size classes. In other words, smaller lizards each prey upon a low number of taxa, but their mutual differences in diet composition tend to be larger than in adults. The increase in individual diversity and decrease of interindividual overlap with size apparently combine into population diversity estimates that do not vary among lizard size groups. Estimates of population diversity were similar in all size classes. This results from opposing trends in the two components of diversity: population evenness decreases, whereas the number of prey types increases with lizard size. Hence, the collection of juvenile stomachs contains fewer prey taxa, but these are more equally represented than in the adults’ stomachs.

The restricted number of prey types captured by the juveniles, both at the individual and group level, is possibly related to the narrow range of prey sizes, and ultimately to restrictions imposed by body size of the younger lizards. During ontogeny, lizards capture increasingly larger prey, but they do not exclude smaller items from their diet. Similar observations have been reported in other lacertid lizards (e.g., Nouira and Mou, 1982; Mou and Baurault, 1986; Mou, 1987). The frequency with which adult *L. lepida* take large invertebrate or vertebrate prey, remains however low.

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