The use of regression equations for the estimation of prey length and biomass in diet studies of insectivore vertebrates

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The use of regression equations for estimation of prey length and biomass in diet studies of insectivore vertebrates.– This work presents two series of allometric regression equations for the estimation of arthropod body length and mass from recognizable remains in food samples of vertebrates. The utility of the equations is tested by analysing faeces from a reptile species *Tarentola mauritanica*. The application of these equations greatly increases the number of prey for which body length and biomass is estimated. Consequently, the application of regression equations is encouraged for diet studies, although it is also advisable either to previously test the applicability of published equations or to develop new equations if necessary.

Key words: Arthropoda, Body length, Body weight, Diet studies, Ecological methods, Regression equations.

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Introduction

Studies on diet analysis are necessary to understand the ecology of most organisms. Nevertheless, the methodology of diet analysis is often questionable and even inaccurate or lax. In birds, for instance, diet is sometimes not directly measured, but assumed from morphology, behaviour, or prey availability (Rosenberg & Cooper, 1990). In the best cases, diet studies consist simply of a qualitative and quantitative description of diet composition. Only recently has there been an increasing interest in more detailed diet information, and methodology has improved to provide the diet description in terms of biomass or prey size, in order to evaluate how profitable the diet is to a given animal (Rosenberg & Cooper, 1990). Insects, and arthropods in general, deserve special attention in this sense because of the importance of the latter as food for a variety of animals (and even plants, Zamora, 1995). One difficulty is, however, that direct measuring and weighing of the prey is usually impossible because prey specimens are often fragmentary, due to manipulation or digestion by predators. Complete prey can be found only at times, e.g. in studies based on stomach-content analysis. However, as these aggressive techniques imply sacrificing the animal studied, researchers tend to avoid their use. In contrast, non-aggressive techniques, such as faecal analysis, are widely accepted, but offer only prey remains to estimate the prey biometry. Under these circumstances, techniques to estimate arthropod length and biomass from a variety of morphological data constitute valuable tools for ecological studies.

In the literature, these estimates have been performed by means of widely differing procedures, restricted at times rather to a specific subject (Herrera, 1978; Calver & Wooller, 1982; Smiley & Wisdom, 1982). The most common procedures have been estimations from the mean of each taxonomic group (ignoring the individual weight variance) or the application of regression equations from lineal measurements (Rogers et al., 1976; Rogers et al., 1977; Schoener, 1980; Gowing & Recher, 1984; Sample et al., 1993). In this latter case however, the prey remains do not always allow measurement of prey body length, which is needed for the application of the equation. An improvement in this procedure has been the use of equations estimating both body length and mass from measurements of characteristic parts of the prey, still recognizable among the remains usual found in a diet study (Calver & Wooller, 1982; Díaz & Díaz, 1990). Despite its considerable utility, this procedure is still not widely employed by many researchers.

The aim of the present study is to demonstrate the utility of these equations in standard studies of diet analysis of insectivorous vertebrates, and the advantage of their availability, even when it is necessary to develop them.

Material and methods

Arthropod sampling and laboratory procedure

The methodology followed both in the field sampling and the lab procedure was the same as in Hódar (1996), and will be described here only briefly. Arthropods were caught during the period 1990-1992, mainly in three different zones of the Guadix-Baza Basin (Granada province, south-eastern Spain), and stored in Scheerpeltz preservative. From this collection, 41 groups were selected, both because of their numerical significance in the arthropod community sampled and their role as prey for different species of insectivorous birds and reptiles. Selection was made based on both the taxonomy (mainly Order, following Barrientos, 1988) and the morphological characteristics of specimens. In hemimetabolous insects, nymphs and imago were pooled, whereas in holometabolous, equations were performed with larvae and imago were separated. Heteroptera was subdivided into "heavy" and "slender", the former for insects with heavy and wide bodies (e.g. Scuterellidae) and the latter for those with slender and light bodies (e.g. Reduviidae). Homoptera did not include Aphidae, Hymenoptera did not include Formicidae.

The term OTU (Operational Taxonomic Unit, sensu Sneath & Sokal, 1973) was used to define these 41 groups. The specimens included in the regression calculations were arbitrarily selected within the body-size gra-

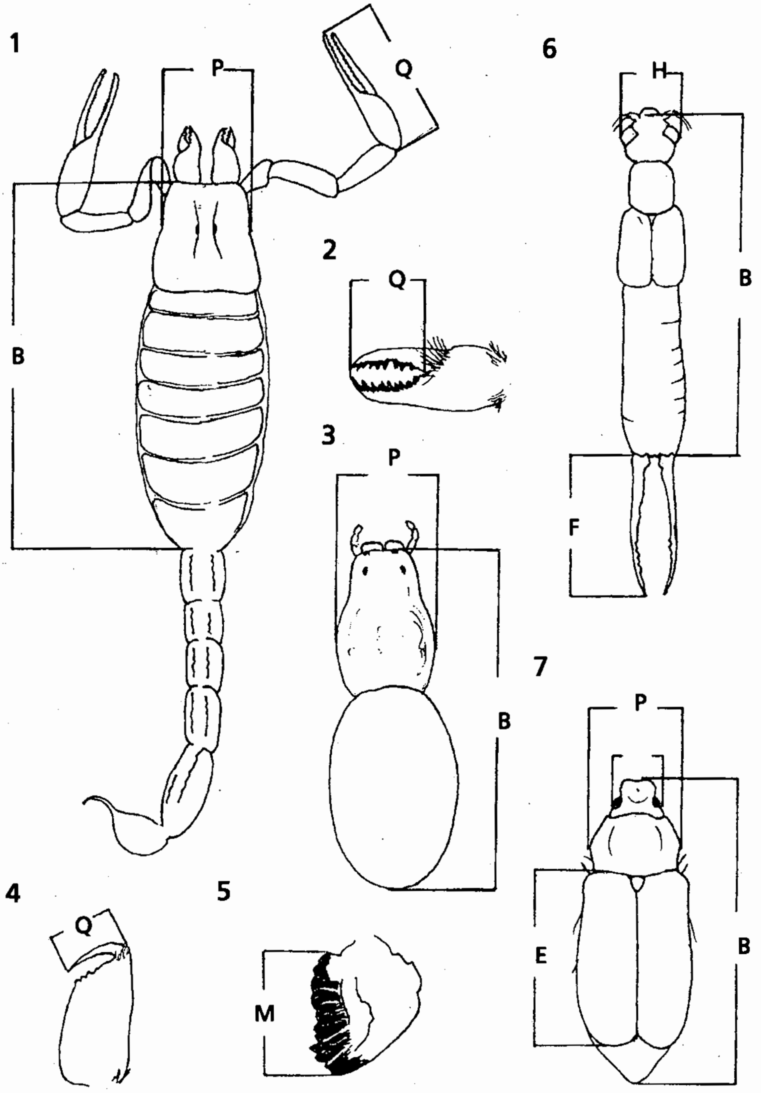

Fig. 1. Examples of the measurements taken on the arthropod bodies. Arthropods are represented without legs for simplicity: 1. Scorpionida; 2. Soliphuga chelicera; 3. Araneae; 4. Araneae chelicera; 5. Lepidoptera larva mandible; 6. Dermaptera; 7. Coleoptera; B. Body length; P. Pronotum or prosoma width; Q. Chelicera; F. Forceps or caudal appendages; H. Head width; E. Elytrum length; M. Mandible.

Ejemplos de las medidas tomadas en los cuerpos de los artrópodos. Los ejemplares se representan sin patas por simplicidad. 1. Scorpionida; 2. Quelícero de Soliphuga, 3. Araneae; 4. Quelícero de Araneae; 5. Mandíbula de larva de Lepidoptera; 6. Dermaptera; 7. Coleoptera; B. Longitud del cuerpo; P. Anchura del pronoto o del prosoma; Q. Quelícero; F. Forceps o apéndices caudales; H. Anchura de la cabeza; E. Longitud del élitro; M. Mandíbula.

dient of the appropriate OTU, in an effort to cover the gradient as fully as possible.

For each individual, the total body length (B) without appendages was measured. Specimens were then dried in an oven at 70°C for 24 h and weighed with an electronic scale (precision 0.01 mg). Measurements were made mainly with a binocular microscope 10-40x with an ocular micrometer, and sometimes with a digital calliper, both with 0.05 mm precision. Once weighed, specimens were rehumidified, and several body parts were measured, depending on the OTU to which the specimen belonged. The parts selected were those usually remaining recognizable and measurable after the passage through the digestive tract of an insectivore (Ralph et al., 1985; Moreby, 1988; pers. obs.). These measurements were (fig. 1): H. Maximum head width, including ommatidia; P. Maximum prosoma or pronotum width, except in Scorpionida, at the eye level; E. Elytron length, measured from the humeral calus to the tip, in Coleoptera; Q. Chelycera length, in Scorpionida, total length of the pedipalp claw; in Araneae, chelicera claw length; in Soliphuga, chelicera jagged part; F. Total length of the forceps or caudal appendages, in Dermaptera; M. Length of the jagged part of the mandible, in Orthoptera and Lepidoptera larvae.

Statistical analysis

Regressions were performed with data transformed to logarithms. This procedure usually normalizes and reduces heteroscedasticity of the data (Edwards, 1985; Zar, 1996). The regression analysis used with the transformed data was always linear. However, since there were equations estimating body weight from length measurements, but also equations estimating body length from length measurements, two types of equations were performed. In the first case, a linear regression $\ln W = \ln A + B (\ln L)$ was first performed and then transformed to a power equation $W = a L^b$ (W being individual dry mass, L any of the measurements taken in the arthropods, and $\ln A = a$ and $B = b$ the parameters), since the length of body fragments has a linear measurement (L^1), whereas weight may be assimilated to a cubic measurement (L^3). Several authors compared different equation models, showing that body mass estimation from a linear measurement fits an exponential equation better than a lineal or other type of measurement (see e.g. Schoener, 1980; Gowing & Recher, 1984). In the second case, a linear equation $\ln B = a + b (\ln L)$ was used to estimate body length from length of body fragments, and this equation was not transformed because one linear measurement (L^1) was estimated from another linear measurement (L^1) (Díaz & Díaz, 1990). Significance of the regressions was corrected with post-hoc Bonferroni sequential adjustments (Rice, 1989).

The effectiveness of applying these equations is demonstrated using a reptile species, *Tarentola mauritanica*, the diet of which was studied by means of faecal analysis (J. A. Hódar & J. M. Pleguezuelos, in prep.), recording the body fragments from which estimations of both body weight and length were made. Analysis of diet samples followed the usual procedures in these cases: samples were dispersed under a binocular microscope and the remains identified and measured (Rosenberg & Cooper, 1990).

Results and discussion

A total of 473 arthropods were used to develop the equation series used here, implying 473 measurements of body weight and length, and 840 of different body parts. The parameters estimated for the regression equations are shown in the table 1. More than 90% of equations have R^2 values up to 0.8 (80% of the variance explained), and are highly significant. In fact, only two equations were non-significant ($p > 0.05$) after sequential Bonferroni correction. It is also noteworthy that a large number of individuals were not needed to construct significant equations (Díaz & Díaz, 1990; Hódar, 1996).

The diet analysis of *Tarentola mauritanica* offered a total of 543 identified prey, from which body size and weight was determined in 417 (76.8%). However, the prey was found complete and could be directly measured in only 27 cases (5.0%); and in four cases (0.7%) the prey was recognized to the species level but no measurement was possible. Therefore the average length for the prey species in the study area had to be assigned. In contrast, measurements taken from remains found

Table 1. Parameter estimates for regression of weight (mg) on other lengths (mm, dependent = W. Weight) with a power model W= aL^b, and of body length on other lengths (both in mm, dependent = B. Body length) with a linear model (lnB)= a+b(lnL) for the 41 OTUs considered. The measurement used as predictor is the column x: H. Head width; P. Pronotum or prosoma width; E. Elytra length; F. Caudal appendages length; Q. Chelicera length; M. Mandible length. R^2. Coefficient of determination; SEE. Standard error of the estimate; SE. Standard error of the parameters a and b (indicated as subindices); n. Sample size.

Parámetros estimados en las regresiones de peso del cuerpo (mg) a partir de otras longitudes (mm, dependiente = W. Peso) con un modelo exponencial W= aL^b, y de longitud del cuerpo a partir de otras longitudes (ambas en mm, dependiente = B. Longitud del cuerpo) con un modelo lineal (lnB)= a+b(lnL) para los 41 OTUs considerados. La medida usada como predictor es la columna x: H. Anchura de cabeza; P. Anchura del pronoto o prosoma; E. Longitud del élitro; F. Longitud de los apéndices caudales; Q. Longitud del quelícero; M. Longitud de la mandíbula). R^2. Coeficiente de determinación; SEE. Error estándar de la estima; SE. Error estándar de los parámetros a y b (indicados como subíndices); n. Tamaño de muestra.

		Body weight estimation						Body length estimation					
X	n	R^2	SEE	a	SE_{lna}	b	E_b	R2	SEE	a	SE_{lna}	b	SE_{lnb}
Scorpionida													
P	7	0.984	0.163	1.136	0.286	3.667	0.207	0.901	0.116	1.559	0.204	0.994	0.148
Q	7	0.973	0.215	0.162	0.524	3.319	0.249	0.890	0.123	1.032	0.299	0.900	0.142
Soliphuga													
Q	6	0.954	0.137	7.327	0.247	2.500	0.318	0.977	0.049	2.153	0.067	0.987	0.076
Araneae													
P	18	0.879	0.753	1.232	0.216	2.375	0.220	0.966	0.163	1.081	0.047	1.024	0.048
Q	10	0.681	1.023	33.435	0.347	1.931	0.467	0.945	0.142	2.491	0.048	0.761	0.065
Isopoda													
H	10	0.961	0.368	0.666	0.226	3.292	0.233	0.909	0.195	1.519	0.120	1.103	0.123
Diplopoda													
H	10	0.975	0.371	0.910	0.215	5.573	0.317	0.851	0.187	2.376	0.127	1.227	0.181
Chilopoda													
H	10	0.982	0.297	1.681	0.149	3.603	0.171	0.852	0.315	2.437	0.158	1.227	0.181
Tisanura													
H	10	0.860	0.280	1.236	0.100	0.975	0.139	0.708	0.245	1.777	0.087	0.535	0.122
Caelifera													
M	17	0.948	0.423	20.436	0.106	3.056	0.185	0.932	0.173	2.662	0.043	1.090	0.076
Blattodea													
H	10	0.846	0.399	1.275	0.210	3.344	0.505	0.928	0.110	1.390	0.058	1.415	0.139
Mantodea													
H	10	0.941	0.440	0.122	0.550	4.240	0.374	0.883	0.199	1.614	0.249	1.320	0.170

Tabla 1 (cont.)

		Body weight estimation						Body length estimation					
X	n	R^2	SEE	a	SE_{lna}	b	SE_b	R^2	SEE	a	SE_{lna}	b	SE_{lnb}
Dermaptera													
H	10	0.929	0.491	0.345	0.423	5.379	0.563	0.957	0.105	1.602	0.081	1.493	0.112
F	10	0.884	0.613	0.598	0.433	2.387	0.306	0.907	0.154	1.726	0.109	0.678	0.077
Embioptera													
H	10	0.940	0.342	0.860	0.118	2.416	0.216	0.956	0.092	2.103	0.032	0.769	0.059
Homoptera													
H	12	0.916	0.571	0.534	0.228	2.715	0.260	0.952	0.174	0.990	0.069	1.116	0.079
Heteroptera "heavy"													
H	11	0.793	0.511	4.238	0.260	2.664	0.454	0.715	0.206	1.701	0.105	0.872	0.184
P	11	0.960	0.224	0.284	0.276	2.576	0.175	0.969	0.068	0.742	0.083	0.892	0.053
Heteroptera "slender"													
H	10	0.781	0.655	3.860	0.209	2.618	0.491	0.771	0.274	1.917	0.088	1.065	0.206
P	10	0.862	0.520	0.502	0.351	2.485	0.352	0.846	0.225	1.090	0.152	1.008	0.152
Nematocera													
H	10	0.940	0.552	3.942	0.259	3.106	0.278	0.944	0.251	2.503	0.118	1.473	0.126
Brachycera													
H	26	0.933	0.469	0.655	0.105	2.526	0.139	0.973	0.111	1.168	0.025	0.958	0.033
Lepidoptera larvae													
H	16	0.749	0.732	5.532	0.272	2.129	0.330	0.834	0.224	2.409	0.083	0.846	0.101
M	9	0.786	0.670	74.084	0.241	2.308	0.455	0.797	0.247	3.406	0.889	0.879	0.168
Ropalocera													
H	10	0.831	0.485	1.634	0.460	2.793	0.446	0.732	0.206	1.830	0.196	0.888	0.190
Heterocera													
H	10	0.946	0.493	2.053	0.250	2.804	0.236	0.969	0.121	1.803	0.061	0.911	0.058
Neuroptera													
H	10	0.966	0.344	0.773	0.159	2.829	0.189	0.803	0.320	1.792	0.208	1.412	0.248
Carabidae larvae													
H	10	0.425	1.158	2.591	0.648	2.341	0.963	0.576	0.434	1.493	0.243	1.198	0.361
Scarabeidae larvae													
H	10	0.925	0.749	1.190	0.393	3.277	0.330	0.951	0.216	1.675	0.113	1.186	0.095
Tenebrionidae larvae													
H	9	0.747	0.642	4.796	0.307	1.701	0.374	0.904	0.127	2.471	0.061	0.604	0.074
Carabidae													
H	12	0.968	0.373	1.258	0.186	3.560	0.206	0.937	0.159	1.603	0.080	1.069	0.088
P	12	0.942	0.498	0.649	0.295	3.040	0.238	0.874	0.224	1.426	0.133	0.894	0.107
E	12	0.969	0.364	0.041	0.357	3.196	0.180	0.985	0.077	0.530	0.076	0.983	0.038

Tabla 1 (cont.)

		Body weight estimation						Body length estimation					
X	n	R^2	SEE	a	SE_{lna}	b	SE_b	R^2	SEE	a	SE_{lna}	b	SE_{lnb}
Tenebrionidae													
H	16	0.949	0.375	1.102	0.266	3.631	0.225	0.920	0.172	1.205	0.122	1.311	0.103
P	16	0.905	0.511	0.397	0.454	3.068	0.265	0.927	0.165	0.786	0.146	1.138	0.086
E	16	0.964	0.315	0.191	0.308	2.569	0.133	0.989	0.064	0.512	0.062	0.954	0.027
Scarabeidae													
H	10	0.849	0.630	1.533	0.534	2.587	0.385	0.815	0.269	1.206	0.228	0.975	0.164
P	10	0.984	0.208	0.401	0.223	2.513	0.115	0.993	0.051	0.655	0.055	0.971	0.028
E	10	0.985	0.196	0.378	0.213	2.588	0.111	0.997	0.033	0.630	0.036	1.001	0.019
Chrysomelidae													
H	10	0.964	0.450	1.343	0.251	3.270	0.301	0.896	0.174	1.328	0.100	0.994	0.120
P	10	0.947	0.412	0.513	0.299	2.791	0.234	0.882	0.191	1.048	0.139	0.837	0.109
E	10	0.925	0.488	0.070	0.545	3.006	0.302	0.965	0.103	0.357	0.115	0.954	0.064
Curculionidae													
P	12	0.877	0.678	1.416	0.284	2.710	0.320	0.935	0.205	1.089	0.086	1.166	0.097
E	12	0.853	0.741	0.319	0.474	2.250	0.295	0.987	0.092	0.392	0.059	1.008	0.037
Aphodiidae													
H	10	0.965	0.254	1.045	0.136	2.803	0.188	0.963	0.091	1.339	0.049	0.974	0.067
P	10	0.955	0.291	0.500	0.205	2.452	0.189	0.962	0.093	1.078	0.065	0.856	0.060
E	10	0.954	0.294	0.078	0.345	3.111	0.243	0.966	0.088	0.420	0.103	1.089	0.073
Cetoniidae													
H	10	0.837	0.468	2.460	0.506	3.526	0.550	0.828	0.141	1.655	0.152	1.027	0.166
P	10	0.945	0.273	0.699	0.383	2.711	0.232	0.970	0.059	1.264	0.082	0.805	0.050
E	10	0.897	0.372	0.147	0.718	2.803	0.336	0.891	0.112	0.831	0.217	0.818	0.101
Dynastidae													
H	10	0.961	0.361	1.633	0.329	3.167	0.226	0.939	0.162	1.332	0.147	1.119	0.101
P	10	0.954	0.393	0.336	0.476	2.892	0.225	0.814	0.282	0.910	0.342	0.955	0.162
E	10	0.885	0.618	0.195	0.844	2.682	0.342	0.978	0.098	0.436	0.133	1.007	0.054
Histeridae													
H	10	0.902	0.367	5.620	0.148	2.284	0.266	0.964	0.078	1.706	0.031	0.820	0.056
P	10	0.964	0.222	0.420	0.242	2.657	0.181	0.923	0.113	0.840	0.123	0.903	0.092
E	10	0.903	0.365	0.591	0.372	2.554	0.297	0.900	0.130	0.935	0.132	0.886	0.105
Buprestidae													
H	10	0.989	0.196	1.035	0.113	3.727	0.137	0.984	0.075	1.453	0.043	1.168	0.052
P	10	0.996	0.126	0.386	0.093	3.053	0.072	0.985	0.073	1.146	0.054	0.954	0.042
E	10	0.996	0.126	0.031	0.150	3.105	0.073	0.997	0.032	0.343	0.038	0.976	0.018

Tabla 1 (cont.)

		Body weight estimation						Body length estimation					
X	n	R^2	SEE	a	SE_{lna}	b	SE_b	R^2	SEE	a	SE_{lna}	b	SE_{lnb}
Cerambycidae													
H	10	0.976	0.246	2.686	0.186	2.941	0.162	0.911	0.165	1.780	0.125	0.980	0.109
P	10	0.985	0.199	1.803	0.166	2.706	0.120	0.952	0.121	1.626	0.101	0.919	0.073
E	10	0.964	0.307	0.034	0.520	3.072	0.212	0.984	0.070	0.210	0.119	1.072	0.048
Meloidae													
H	10	0.953	0.380	1.270	0.323	3.260	0.256	0.959	0.141	1.519	0.120	1.293	0.095
P	10	0.937	0.439	1.164	0.383	3.501	0.320	0.974	0.113	1.460	0.099	1.411	0.082
E	10	0.446	1.305	0.003	3.974	4.589	1.807	0.469	0.505	-1.032	1.539	1.860	0.700
Staphylinidae													
H	10	0.983	0.377	1.309	0.149	2.642	0.124	0.943	0.197	1.938	0.078	0.744	0.065
P	10	0.988	0.312	0.867	0.134	2.963	0.115	0.938	0.204	1.825	0.087	0.830	0.075
E	10	0.982	0.387	0.534	0.182	3.067	0.148	0.915	0.239	1.697	0.113	0.852	0.092
Coleoptera others													
H	16	0.949	0.343	2.014	0.098	2.891	0.180	0.910	0.195	1.585	0.056	1.212	0.102
P	16	0.859	0.568	1.084	0.206	2.093	0.227	0.663	0.376	1.385	0.136	0.788	0.150
E	16	0.895	0.491	0.150	0.332	2.244	0.206	0.955	0.138	0.418	0.093	0.993	0.058
Hymenoptera													
H	24	0.919	0.514	1.999	0.112	2.090	0.132	0.964	0.170	1.332	0.037	1.053	0.044
Formicidae workers													
H	11	0.982	0.192	0.552	0.068	2.550	0.116	0.893	0.160	1.463	0.057	0.839	0.097
Formicidae winged													
H	10	0.938	0.305	1.607	0.127	2.752	0.250	0.846	0.123	1.825	0.051	0.672	0.101

in the faeces allowed the estimation of another 384 prey (70.7%).

Head width was the most useful measurement to predict prey length and mass (283 prey, 52.1 % of cases), as in most insects, the head is a very sclerotized part of the body, and thus resistant to digestion. However, it is also very recognizable. Other undigestible parts more difficult to recognize such, as the elytra (33 prey, 6.1% of cases) and mandibles (33 prey, 6.1% of cases) proved to be second in usefulness. These results exemplify that regression equations increase the quantity of prey for which body length and weight can be estimated.

However, as regression equations are clearly not equally applicable in geographical zones other than those where the equations were developed, it is advisable that new equations be developed when working in a zone for which no equations are available and the similarity with other equations has not been tested (SCHOENER, 1980; HÓDAR, 1996). In any case, it is not necessary to make an estimation of every arthropod group present in the zone: a complete series of equations, as presented in table 1, is useful for broad studies involving several species at the same site (HÓDAR, 1993, 1994, 1995; HÓDAR et al., 1996). However, in more specific works, it is feasible first to perform the diet analysis, identifying the main taxonomic groups in the diet, and taking the appropriate measurements from their remains (CALVER & WOOLLER, 1982; RALPH et al., 1985; MOREBY, 1988; DÍAZ & DÍAZ, 1990). Equations can then be developed for only those groups and parts that are required. This procedure reduces the bulk of work and ensures a good adjustment of the estimates. For instance, in the present example of *T. mauritanica*, 73.9% of the estimates (308 prey, 56.7% of identified prey) were made with only eight equations (estimates from Lepidoptera larva mandible length and head width, Dermaptera head width, Araneae cephalothorax width, Formicidae head width, Curculionidae elytra, other Coleoptera elytra, and Homoptera head width), which implied biometry for only 95 arthropods (175 measurements and 95 weighings).

In conclusion, regression equations are a valuable tool to estimate both the length and mass of the arthropod prey of insectivorous species. However, correct application requires a good knowledge of entomology by ecologists in general (MORRISON et al., 1990), in addition to care and rigor in the application. Even when accurate, this tool cannot compensate for incorrect or careless application (HÓDAR, 1996). As ROSENBERG & COOPER (1990) pointed out, "many of the biases and difficulties (on avian diet analysis) will be alleviated when more careful attention is paid to sampling design, prey identification, and overall foraging ecology." Regression equations may be an important help in this sense.

Resumen

El uso y la utilidad de ecuaciones de regresión para la estima de longitud y biomasa de presas en estudios de dieta de vertebrados insectívoros

Este trabajo presenta dos series de ecuaciones alométricas (tabla 1) que permiten estimar la longitud y el peso de artrópodos que forman parte de la dieta de vertebrados a partir de los restos encontrados en las muestras alimenticias de estos predadores (fig. 1). La utilidad de estas ecuaciones se ha ejemplificado mediante su aplicación a un análisis de muestras alimenticias (excrementos) de salamanquesa común (*Tarentola mauritanica*), incrementando desde el 5.7% al 76.8% el número de presas para las cuales longitud y biomasa es conocido. En consecuencia, se sugiere la aplicación de ecuaciones alométricas en estudios de dieta como un procedimiento que permite aumentar la cantidad y calidad de la información obtenida, pero se recomienda comprobar la aplicabilidad de las ecuaciones disponibles o crear nuevas series de ecuaciones.

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