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BODY MASS AND TROPHIC LEVEL VARIATIONS IN RELATION TO HABITAT DISTURBANCE IN A SET OF MAMMAL SPECIES

C. BATTISTI[1*], *G. FANELLI*[2], *F. CERFOLLI*[3], *G. AMORI*[4], *L. LUISELLI*[5]

[1] *"Torre Flavia" LTER (Long Term Ecological Research) Station, Città Metropolitana di Roma, Parks Service, Via Tiburtina, 691, 00159 Rome, Italy*
[2] *Dipartimento di Biologia, Università degli studi di Roma Tor Vergata, via della Ricerca Scientifica, 00133 Rome, Italy*
[3] *Department of Ecology and Biology Sciences (DEB), Tuscia University, Largo dell'Università, snc, Blocco C, 01100 Viterbo, Italy*
[4] *CNR Institute of Ecosystem Studies, Viale dell'Università 32, 00185 Rome, Italy*
[5] *IDECC, Institute for Development, Ecology, Conservation and Cooperation, Via G. Tomasi di Lampedusa 33, 00144 Rome, Italy and Department of Applied and Environmental Biology, Rivers State University of Science and Technology, PMB 5080, Port Harcourt, Rivers State, Nigeria*
** Corresponding author: c.battisti@cittametropolitanaroma.gov.it*

HEMEROBY
SPECIES TRAITS
ATLAS DATA
MAMMALS

ABSTRACT. – We tested whether the species linked to progressively disturbed environments differed in terms of their body size and trophic level. We used a set of mammal species from a region of central Italy (Latium), for which both a representative amount of data (> 30 records) and their habitat preferences were obtained from a regional atlas. To assess the level of disturbance, we used the hemeroby index (HS). We categorized the focal mammals in three groups subdivided by their body size (small, medium, large) and trophic level (omnivorous, herbivorous, predators), and applied a suite of statistical analyses, including GLM modeling. We observed that at the increase of species' body mass, the HS index significantly decreased, while no significant changes occurred when using the categories of trophic level. Species inhabiting or colonizing disturbed habitats are usually r-strategists with high dispersal rates and rapid recruitment, traits often associated to small body size. There was also no correlation between body size and trophic level by species.

INTRODUCTION

Community structure is influenced by many factors, including abiotic factors, species interactions, chance events, and level of disturbance (Ricklefs & Miller 1999). In animal communities, the degree of coexistence and the diversity patterns may be largely determined by the level of specialization (or generalism) of co-occurring species, as well as by their interactions, with interspecific competition being among the primary assembling forces (Connell 1978, Huston 1994, Crandall *et al.* 2003, Barnagaud *et al.* 2011). The structure of animal communities, however, is not stable in time and space, and can be disrupted by disturbance, often in a non-linear way, with disturbance processes challenging both the community functioning at different ecological levels, from individuals to populations, and even up to ecosystems (White 1979, Pickett & White 1984, review in Battisti *et al.* 2016).

A large number of hypotheses explaining the structural characteristics of ecological communities and the assembly rules have been proposed, including chance/competition (Diamond 1975, Connor & Simberloff 1979), niche theory (Chase & Leibold 2003, Schoener 2009, Townsend *et al.* 2011), island biogeography theory (MacArthur & Wilson 1967, Wilson 2010), the unified neutral theory of biodiversity and biogeography (Hubbell 2011), and the food web theory (Pimm 1992, McDonald-Madden *et al.* 2016, review in Weiher & Keddy 2001). Among them, the intermediate disturbance hypothesis suggests that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Wilkinson 1999). According to this hypothesis, at intermediate levels of disturbance, diversity is maximized because species thriving at both early and late successional stages can coexist (Wilkinson 1999). At a structural level, species richness can be affected by disturbance processes in ways that are often non-linear: for example, in the intermediate disturbance hypothesis at the level of assemblages of species, the degree of coexistence and diversity may be largely determined by the level of specialization (or generalism) of co-occurring species (Connell 1978, Huston 1994, Crandall *et al.* 2003, Barnagaud *et al.* 2011). In this model, the effect of disturbance on a given community depends on the intensity, frequency duration and extension of the disturbance regime (Sousa 1984).

When disturbances have low intensity, frequency or duration, the communities tend to be relatively stable and dominated by more specialized species whereas when disturbances are high, the communities tend to be unstable and dominated by generalist species (Sousa 1984, Mouillot *et al.* 2013).

Some ecological traits can be used as predictors of sensitivity to disturbance for a given species (Mouillot *et al.* 2013), for instance, body size and trophic level (e.g.

Ewers & Didham 2006). Large species become rarer in communities impacted by anthropogenic stress, whereas the increase in the frequency or intensity of a given disturbance factor determines an increase in the density of small species (Swihart *et al*. 2003). Disturbance has also effects on the trophic hierarchy of the community, as its intensity and frequency increase often induces a simplification with the disappearance of the higher trophic levels (Menge & Sutherland 1987, Power *et al*. 1995, Williams & Martinez 2004, Borrelli & Ginzburg 2014).

Distribution of body size among (animal) species within a community is not random and many hypotheses linked to energy, phylogeny and eco-biogeography (Blackburn *et al*. 1999, Rohde 1999, Allen *et al*. 2006) have been advanced to explain the observed pattern. In mammals, the distribution of body size influences the home range size (Lindstedt *et al*. 1986, Kelt & Van Vuren 1999, Ottaviani *et al*. 2006) and the dispersal rate (Santini *et al*. 2013) but it has also been shown that it is influenced by latitude (Blackburn & Hawkins 2004), population density (e.g. Silva & Downing 1995, Blackburn & Gaston 1999, Amori *et al*. 2015), and metabolic rate (Hennemann 1983). Anthropogenic disturbance may affect body size (Ewers & Didham 2006), but there are no studies on mammals that analyze whether mean body size is different at different levels of disturbance. It is however difficult to define univocally the disturbance regimes (Salafsky *et al*. 2003, 2008, Balmford *et al*. 2009, Battisti *et al*. 2016).

In the last decades, an useful approach to define and quantify the disturbance regimes has been utilized in plant ecology applying the concept of hemeroby to evaluate the distance of a system from less disturbed conditions (van der Maarel 1975, Kowarik 1989, 2006, McDonnel & Pickett 1990, Hill *et al*. 2002, Fanelli *et al*. 2005). Hemeroby broadly corresponds to the position of the optimal niche of a given species along the gradient from least disturbed to heavily disturbed habitat types (Grabherr *et al*. 1998, Steinhardt *et al*. 1999, Testi *et al*. 2009, Schleupner & Schenider 2013). Recently, the concept of hemeroby has been applied also to animal ecology (birds: Fanelli & Battisti 2015, Battisti & Fanelli 2016, mammals: Battisti *et al*. 2017; review and comparisons in Battisti & Fanelli 2018). The application of the hemeroby concept, according to these studies, appears to be effective in homeotherm vertebrates like it is in plants, as it allows detecting even fine-grained levels of disturbance that overcome animal communities (Battisti *et al*. 2019).

Mammals comprise a large number of species inhabiting different habitat types, ranging from strictly specialized species to broad generalists, and showing different levels of adaptation and response to natural and anthropogenic disturbances (Macdonald 2009). The level of sensitivity of mammals to disturbance is indirectly related to the level of disturbance experienced by the habitat where the species occur. In this regard, we may distinguish species linked only to less-disturbed habitats from species that dominate in heavily human-transformed habitats (for historical disturbance-driven extinctions of more sensitive species, see Gippoliti & Amori 2006).

On the basis of the distribution data of mammal species in a given region, that is generally achieved through atlases, it is possible to attribute to each species a given hemeroby level. Indeed, from the atlas data, it is possible to link a given species to given vegetation preferences, and this linkage makes possible, for those species for which a representative amount of data are available, to calculate an index of the average level of disturbance tolerated by each species (hemeroby score, HS; Battisti & Fanelli 2018).

In this paper, using the above-mentioned "hemeroby concept" applied to a regional context (mammals of Latium, central Italy), we test the following key questions: (i) Do the species linked to progressively more disturbed environments show a progressive reduction in their body size? (ii) Do the species linked to progressively more disturbed environments show a progressive reduction in their trophic level? (iii) Are body size and trophic levels correlated?

METHODS

Study area: The study area was the administrative region of Latium, extending over 17,000 km^2 in Central Italy, with about 5,100,000 people – mostly living in Rome and surrounding area – and an average density of 297 inhabitants per km^2. The study area extends from the Apennines to the Tyrrhenian Sea and is characterized by a high landscape heterogeneity due to a varied geology (limestones, sandstones, clays, volcanic and alluvial rocks), orography and geomorphology. Mountains represent 26 % of the area, hills 54 %, and lowlands 20 % (Regione Lazio 2000, 2004). Land soil use is 10 % urban and industrial 98 % agricultural and only 2 % natural areas (including waters; Regione Lazio 2004).

Data Sampling: In the study area, 71 species of mammals have been recorded, and their local distribution is available in Capizzi *et al*. (2012). As explained in Capizzi *et al*. (2012), distribution data for the various species were obtained by trained personnel (especially park rangers, voluntary experts, professional zoologists) by means of either a large number of original sampling techniques (direct observations, indirect tracks, traps, owl pellets, marking and recapture, road investments) or by reviewing historical data deposited in protected areas, universities, public authorities, museum, and private subjects.

For our study, we selected only those species (n = 48; Table I) with > 30 independent distribution records to avoid bias in observer skill that may play an important role (Sutherland 2006, further details in Capizzi *et al*. 2012; about data reliability see also Battisti *et al*. 2014). Taxonomic nomenclature followed Amori *et al*. (2009).

Table I. – Hemeroby score (HS) values for each mammal species selected and related scores of body mass and trophic level.

Species	HS	Body mass	Trophic level
Rattus norvegicus	8.352	1	1
Mus musculus domesticus	7.473	1	1
Rattus rattus	7.040	1	1
Sus scrofa	2.520	3	1
Microtus savi	7.032	1	2
Apodemus sylvaticus	5.452	1	2
Muscardinus avellanarius	5.166	1	2
Sciurus vulgaris	3.513	1	2
Glis glis	3.347	1	2
Apodemus flavicollis	3.210	1	2
Myodes glareolus	3.040	1	2
Myocastor coypus	7.589	2	2
Oryctolagus cuniculus	6.879	2	2
Hystrix cristata	5.368	2	2
Lepus europaeus	3.066	2	2
Lepus corsicanus	2.747	2	2
Dama dama	2.374	3	2
Capreolus capreolus	1.687	3	2
Cervus elaphus	1.519	3	2
Rupicapra pyrenaica ornata	1.397	3	2
Sorex samniticus	7.682	1	3
Erinaceus europaeus	7.672	1	3
Suncus etruscus	7.511	1	3
Crocidura leucodon	7.158	1	3
Myotis daubentonii	6.865	1	3
Tadarida taeniotis	6.852	1	3
Crocidura suaveolens	6.786	1	3
Talpa romana	6.691	1	3
Hypsugus savi	6.397	1	3
Pipistrellus kuhlii	6.395	1	3
Mustela nivalis	6.136	1	3
Nyctalus leisleri	3.999	1	3
Pipistrellus pipistrellus	3.971	1	3
Myotis emarginatus	3.904	1	3
Miniopterus schreibersi	3.876	1	3
Eptesicus serotinus	3.753	1	3
Rhinolophus ferrumequinum	3.736	1	3
Pipistrellus pygmaues	3.127	1	3
Rhinolophus hipposideros	3.120	1	3
Vulpes vulpes	5.709	2	3
Meles meles	5.211	2	3
Mustela putorius	4.376	2	3
Martes foina	3.919	2	3
Neovison vison	3.131	2	3
Martes martes	3.016	2	3
Felis sylvestris	1.758	2	3
Canis lupus	1.832	3	3
Ursus arctos	1.736	3	3

For each distributional record, we computed the sum of the area of each Corine Land Cover habitat type (levels 4 and 5) around a species-specific buffer (see Battisti *et al*. 2017 for specifications on the buffer size for each species), by using Quantum GIS software (version 1.8.0; QGIS Development Team 2015). Thus, we obtained a species/habitat type matrix that was used for all the calculations. Since each habitat type has a specific level of disturbance that may be expressed with its specific hemeroby score (Enzenhofer *et al*. 2009), it is possible to order the habitat types along a gradient from less disturbed habitats without anthropogenic disturbance to completely artificial habitats, where synanthropic plants are dominant (Jalas 1955, Kowarik 1989, Battisti & Fanelli 2015). Hemeroby can be expressed at different scales (Rüdisser *et al*. 2012, Walz & Stein 2014, Eurostat 2016). In this paper we classified habitats by a rank of 1 = not disturbed to 10 = highly disturbed. This highly detailed ranking was possible because the habitat classification (n = 116 habitat types) of the atlas is very detailed, thus allowing a fine evaluation of the degree of hemeroby of each habitat type (see Battisti *et al*. 2017 for details).

Data analysis: For each mammal species we calculated the hemeroby score (HS):

$$HS = \sum[(A_{ij} x HS_j)]/A_{tot}$$

where A_{ij} is the total area of habitat j in the buffer made for species i (see Battisti *et al*., 2017 for details), HS_j is the hemeroby score of jth habitat; and A_{tot} is the sum of all areas of all habitats included in buffers around the localization points of species i. This formula is widely used in plant ecology, and represents the weighed average or barycentre of the distribution of the species along the hemerobiotic gradient (Ter Braakand & Barendregt 1986). The mean values (± SD) of HS were subsequently obtained for each of the three body mass categories.

In our analyses, HS was considered as the dependent variable. As independent variables, we used:

(1) average species' body mass (three classes each one with a categorical score: 1 = species having a mean weight < 1 kg ("small mammals"); 2 = mean weight ranging between > 1 and > 10 kg ("meso mammals"); 3 = species having a mean weight > 10 kg ("large mammals") data from Boitani *et al*. 2003, Amori *et al*. 2008, Aulagner *et al*. 2010;

(2) trophic level (three categories: 1 = mainly omnivorous; 2 = mainly herbivorous; 3 = carnivorous/insectivorous) data from Boitani *et al*. 2003, Amori *et al*. 2008, Aulagnier *et al*. 2008.

Correlation between body size and trophic level by species was tested by Spearman's rank correlation coefficient. In order to compare the mean values of HS among different body mass and trophic level classes we performed a Kruskal-Wallis test followed by Mann-Whitney U tests for pairwise comparisons, using SPSS 13.0 software for Windows (SPSS Inc. 2003). A General Linear Model was used for assessing the effects of the categorical variables (body size and trophic level) on the hemeroby score as dependent variable. In the GLM, the identity link function and a normal distribution of error were used (McCullagh & Nelder 1989), with the Kolmogorov-Smirnov test used to assess the Goodness of Fit ($P > 0.05$) of the GLM model. GLM model was carried out using Statistica software 11.0 version. All tests were two-tailed and P was set at 5 %.

RESULTS

Data on the values of HS, body mass and trophic level for each species are reported in Table I.

There was a significant variation in HS among the three body mass categories (Kruskal-Wallis test: $\chi^2 = 19.239$, df = 2, $p < 0.001$), with small mammals having significantly higher HS than meso- and large mammals (Fig. 1A). However, Kruskal-Wallis test showed no significant differences in HS index as for the categories of trophic level ($\chi^2 = 4.961$, df = 2, $p = 0.084$; Fig. 1B), and Mann-Whitney U-test revealed that there were also no differences when comparing pairs of trophic level categories (LT1 vs LT2: $Z = -1.701$, $p = 0.089$; LT2 vs LT3: $Z = -1.659$, $p = 0.097$; Mann-Whitney U test).

Body size and trophic level were not significantly correlated (Spearman's rank correlation coefficient, $r_s = 0.184$, $p = 0.210$).

The above-mentioned results were confirmed by a GLM model revealing that body size had an effect on the hemeroby score, whereas the same was not true for the trophic level (Table II). In addition, GLM also showed that the interaction term "body size x trophic level" was statistically significant (Table II). Nonetheless, the statistical significance of the interaction term might be due merely to chance as there was a very unbalanced sample sizes across categories.

DISCUSSION

Our study demonstrated three main patterns: (i) significant effect of body size on HS index; (ii) no effect of trophic level on HS index; (iii) no correlation between body size and trophic level by species.

Concerning pattern (i), our study reveals, for the first time to our knowledge, that when species' body size increases, the hemeroby scores decrease: that is, the larger are the species, the more they occur in less disturbed habitats. Body size distributions are often used to describe structure and energy flux in communities and ecosystems (Jennings *et al*. 2001). For example, the relationship between body size and disturbance has been explored in the model of Abundance/Biomass comparisons (Connell 1978, Warwick 1986, Warwick *et al*. 1987), where cumulated frequency curves were used to detect the presence of perturbations. In this model, small-sized species prevail in disturbed habitats (Dauer *et al*. 1993, Magurran 2004 for a review), whereas larger species tend to prevail in more natural environments (for mammals: Prete *et al*. 2012). Our hemeroby approach revealed an analogous pattern between mammal body size and habitat disturbance in the study areas, thus confirming the generality of this relationship. This pattern could be due to different ecological causes. Species inhabiting or colonizing disturbed habitats should be characterized by high dispersal rates and rapid recruitment (r-strategists), i.e. life-history

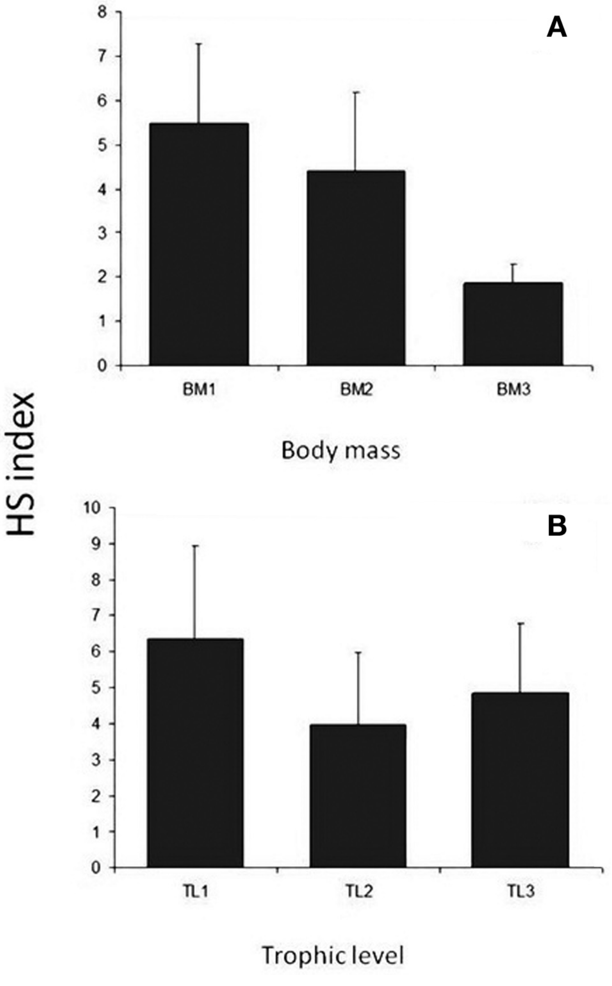

Fig. 1. – Mean (± s.d.) values of HS index for the three body size categories (**A**), and for the three trophic level categories (**B**).

Table II. – Results of a GLM model on the effects of body size, trophic level and their interaction on the hemeroby score for mammal species of Latium, central Italy.

	df	Mean square	F	p
Intercept	1	416510075	161.9613	< 0.001
Body size	2	34749691	13.5125	< 0.001
Trophic level	2	7192099	2.7967	0.072
Body size × Trophic level	2	3257133	5.590	< 0.0001
Error	43	2571665		

traits that generally evolve in small-sized animals. On the contrary, k-strategists with large body size can find their optimal ecological niche and persist with viable populations in less disturbed environments (review in Battisti *et al*. 2016).

The fact that HS index was not influenced by the trophic level of the various species (pattern (ii)) can be explained by a general lack of specialization in the habits of mammalian species in Europe (and in temperate regions in general), with both large predators and large consumers being usually generalists in habitat use (e.g. see Mysterud *et al*. 1999, Lesmerises *et al*. 2012).

Concerning pattern (iii), we speculate that this would depend merely on the broad size range of consumers in Italy (from small rodents to large ungulates) as well as probably in most of the world (Jennings *et al*. 2001; but for the fish exception see Romanuk *et al*. 2011). Indeed, in food webs characterized by a broad range of primary consumers with large body size, apparently there is no relationship between trophic position and body size across taxa (Layman *et al*. 2005).

Although only explorative, this is the first survey analyzing the relationship between two important life-history traits of species and the hemeroby index, as a new metric useful for assessing the level of disturbance occurring where species live. However, our data may have been affected by: (1) the small sample size of a few widespread and presumably common species (i.e. with a high number of atlas data); (2) the aggregation of data in just three ranked categories of body size and trophic level, that can mask more complex trends; (3) the intrinsic features of mammals, that are taxonomically homogeneous but ecologically and phylogenetically very heterogeneous; (4) the fact that hemeroby does not express the disturbance *per se* but the response of the organisms to the whole set of disturbances induced in medium-long times by anthropization (i.e. the level of distance of a habitat from a condition of naturalness).

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