# PREDATOR TROPHIC GUILD ASSIGNMENT: THE IMPORTANCE OF THE METHOD OF DIET QUANTIFICATION

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## RÉSUMÉ

Nous avons évalué les effets respectifs de trois méthodes de quantification des régimes alimentaires (MQRA), basées sur la fréquence d'occurrence des proies, le poids sec des restes de proies et l'estimation de la biomasse fraîche ingérée, sur la classification en guildes de trois espèces de carnivores et sur la base de cinq jeux de données. Les matrices de dissemblance des régimes et la détermination des guildes dépendent de la MQRA choisie. Les deux omnivores (le Renard roux *Vulpes vulpes* et le Blaireau européen *Meles meles*) changeaint de guilde selon la MQRA alors que le Lynx pardelle (*Lynx pardinus*) restait constamment dans la guilde des consommateurs de lapins. Afin de vérifier la généralité de ces incohérences dans la détermination des guildes, nous avons analysé de la même façon six autres communautés de prédateurs. Selon la MQRA retenue, le nombre de guildes reconnues s'est modifié dans quatre des six comparaisons, des changements dans la composition des guildes se sont produits dans tous les cas et le degré moyen de constance dans une guilde n'a été que de $30 \pm 21$ % (n = 6). Le choix de la MQRA dépend de la question écologique posée en préalable à l'analyse des données. Quand le but est d'étudier l'effet des proies sur leurs prédateurs, une estimation de la biomasse consommée semble être le meilleur choix ; en revanche, quand il s'agit d'appréhender les effets des prédateurs sur leurs proies, l'approche basée sur le nombre de proies est alors la plus appropriée.

## SUMMARY

We quantitatively assessed the effect of three Methods of Diet Quantification (MDQ) (based on frequency of occurrence of prey, dry weight of prey remains, or estimation of fresh biomass ingested) on guild classification of three carnivores species based on five data sets. Diet dissimilarity matrices and recognition of trophic guilds were dependent on MDQ. Both omnivorous (Red Fox, *Vulpes vulpes*, and Eurasian Badger, *Meles meles*) shifted to different trophic guilds depending of the MDQ chosen, whereas Iberian Lynx (*Lynx pardinus*) remained consistently in the rabbit-eating guild. As a way to assess the pervasiveness of inconsistencies in guild classification, we applied our approach to six other predator assemblages. The number of recognized guilds shifted as a result of MDQ in 4 of 6 comparisons, changes in guild membership occurred in all assemblages, and mean percentage

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of guildmate fidelity was only 30 % (1SD = ± 21, n = 6). The choice of MDQ depends on the specific ecological question to be addressed with the data. When investigators focus on the effects of prey on predators, an estimate of biomass ingested seems the best choice, but when the focus is on the effects of predators on prey, an approach based on prey numbers is more appropiate.

## INTRODUCTION

The assessment of effects of predators on their prey and effects of prey on their predators are two of the major goals for ecologists interested on food webs (Abrams, 1992; De Ruiter *et al.*, 1996; Winemiller & Polis, 1996). Nevertheless, when focus on empirical food webs, an inadequate dietary information is often a major methodological issue obstructing such assessment (Polis, 1991). For instance, lumping versus splitting as a function of level of biological organization, and the inappropriate incorporation of tropic links are some of those problems (Greene & Jaksic 1983; Schoener, 1989; Martinez, 1991). Less attention has been devoted to the issue of dietary quantification. This is consequential because if different Methods of Diet Quantification (MDQ) lead to contrasting diet estimates, the choice of the MDQ could depend of the ecological question of interest to investigators (e.g., effects of predators on their prey versus effects of prey on their predators).

Guild, defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root, 1967), has became a widely accepted operational unit for the study of investigator-defined assemblages, and has been used to describe the structure and dynamics of food webs (Pianka, 1973; Hawkins & MacMahon, 1989; Jaksic *et al.*, 1996). For predators, guilds usually are based on a trophic dimension (Marti *et al.*, 1993). Nevertheless, estimation of predator diets can be biased as a result of sampling (Real, 1996) or laboratory methodologies (Putman, 1984). Temporal and spatial variation in diet composition are also important sources of bias (Reynolds & Aebischer, 1991), as are methods of diet quantification (Carss & Parkinson, 1996). Diet of predators usually is quantified from post-ingestion remains (feces, pellets, and gastrointestinal contents) because they are relatively numerous and easily collected (Putman, 1984; Marti, 1987; Mills, 1991). MDQs from post-ingestion samples can be grouped into four types: I) methods based on the number of occurrences of prey (i.e. number of samples containing a specific prey type; Rose & Polis, 1998), II) methods based on the number of prey (e.g., Jaksic *et al.*, 1996), III) methods based on the volume or dry weight of prey remains in the sample (e.g., Martin *et al.*, 1995), and IV) estimations of the fresh biomass ingested (e.g., Marti *et al.*, 1993). Thus, inconsistencies in composition of predator trophic guilds as a consequence of MDQ have been predicted (Simberloff & Dayan, 1991), but not empirically demonstrated.

In this paper, we show in detail how diet dissimilarity as well as trophic guild recognition and assignment are sensitive to the choice of MDQ in a local predator assemblage of three mammalian carnivores. Thereafter, we apply our approach to other predator assemblages to illustrate that inconsistencies in guild membership arise as a consequence of MDQ in an ubiquitous manner. Finally, we give some guidelines for the choice of MDQ depending of the ecological question to be addressed with our dietary data.

The study was conducted in the northern portion of the Doñana National Park (37° 9' N, 6° 26' W), located on the west bank of the Guadalquivir River mouth in southwestern Spain. The climate is sub-humid Mediterranean, with a mean annual rainfall of 500-600 mm. Two main biotopes occur within the study area. Scrubland (8 km²) has high cover of vegetation in which *Pistacea lentiscus* is the dominant shrub, and *Quercus suber, Fraxinus* sp. and *Pirus bourgaeana* are the typical species of trees. Pastureland is an open area (3 km²) with scattered *Q. suber* and *Olea europaea*. A more detailed description of the study area and its populations of carnivores is provided by Fedriani *et al.* (1999).

For our exercise, we first used data sets (see Table I) for Red Fox (*Vulpes vulpes*), Eurasian Badger (*Meles meles*), and Iberian Lynx (*Lynx pardinus*). For both fox and badger we used data from each biotope separately, whereas for lynx, which are not abundant in pastureland (Fedriani *et al.*, 1999), we used only data for scrubland. Diet estimations were based on feces collected monthly from November 1992 to December 1994. We analysed a total of 322 fox feces, 279 badger feces, and 240 lynx feces. Prey remains were identified following Reynolds & Aebischer (1991). All identified prey were categorized into 13 prey groups (Table I). The importance of prey types was quantified by three different methods: I) frequency of occurrence (FO) = number of occurrences of each prey type (i.e. number of feces containing each prey type) × 100 / total number of feces; II) dry weight of remains of prey types (DWP) = dry weight of remains of each prey type × 100 / dry weight of total feces; III) fresh biomass ingested (FBI) = dry weight of remains of a particular prey type × its correction factors (CF) × 100 / (dry weight of remains of each prey type × CF of each prey type). Correction factors were obtained from the literature (Lockie, 1959; Aldama, 1993; Martín *et al.*, 1995). Although the use of correction factors for transforming dry into fresh weight data has potential bias (Reynold & Aebischer, 1991), it is a frequent approach in feeding studies of mammalian predators (Jedrzejewski *et al.*, 1992; Martín *et al.*, 1995) given that other methods for the estimation of biomass ingested by predators are not exempted of bias (Rosenberg & Cooper, 1990; Ciucci *et al.*, 1996).

To assess the effect of MDQ on diet dissimilarity, we computed dietary dissimilarity matrices [dissimilarity = 1-Pianka (1973) index of similarity] for each method and evaluated the degree of association among them using Mantel's permutation tests with 5,000 iterations (Manly, 1991). To assess the effect of the MDQ on guild recognition and assignment, we applied cluster analyses to each dissimilarity matrix, thus obtaining three dendrograms. For comparison with previous studies (Jaksic & Delibes, 1987; Marti *et al.*, 1993; Jaksic *et al.*, 1996), we used the unweighted pair-group clustering with arithmetic averaging (Romesburg, 1984) and assumed that a dietary similarity of 50 % was the minimum level to ascribe guild membership. We compared pairs of dendrograms, and estimated the percent of guildmate fidelity (GMF) as: (Number of pairs of guildmates matching in both dendrograms compared) × 100 / (Number of pairs of guildmates matching plus those not matching in both dendrograms (N)). Percent GMF ranges from 0 % (all pairs of guildmates shift) to 100 % (no pair of guildmates shifts). Because the diet of Iberian lynx was known to be based on rabbits, *Oryctolagus cuniculus* (Delibes, 1980), we did not expect shifts in its guild affiliation and we used it as the predator species that consistently would define the rabbit-eating guild.

## TABLE I

*Dietary data used for analysis based on feces collected monthly from November 1992 to December 1994 in Doñana National Park. A total of 322 fox feces, 279 badger feces, and 240 lynx feces were analyzed. Method of diet quantification were: 1) frequency of occurrence (FO) = number of feces containing each prey type × 100 / total number of feces; 2) dry weight of remains of prey types (DWP) = dry weight of remains of each prey type × 100 / dry weight of total feces; 3) estimate of fresh biomass ingested (FBI) = Dry weight of remains of a particular prey type × its correction factors (CF) × 100 / Σ (Dry weight of remains of each prey type × CF of each prey type). Lagom. = Lagomorphs; S. mamm. = small mammals; Artiod. = Artiodactyla; Coleopt. = Coleoptera; Orthopt. = Orthoptera; o. inver. = other invertebrates.*

| | FOX | | | | | | BADGER | | | | | | LYNX | | |
| | Scrubland | | | Pastureland | | | Scrubland | | | Pastureland | | | Scrubland | | |
| | FO¹ | DWP | FBI | FO¹ | DWP | FBI | FO¹ | DWP | FBI | FO¹ | DWP | FBI | FO¹ | DWP | FBI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lagomo. | 50.0 | 34.4 | 48.8 | 52.4 | 40.1 | 56.2 | 38.8 | 25.8 | 61.4 | 15.7 | 9.1 | 33.8 | 99.6 | 99.1 | 98.8 |
| S. mamm. | 7.0 | 2.7 | 2.2 | 6.1 | 1.7 | 1.4 | 7.6 | 2.6 | 3.2 | 4.3 | 1.0 | 1.9 | tr[a] | tr | tr |
| Artiod. | 25.0 | 11.1 | 23.3 | 20.7 | 6.9 | 14.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | tr | tr | tr |
| Birds | 7.0 | 1.2 | 2.1 | 16.5 | 3.41 | 6.3 | 2.4 | tr | tr | 10.0 | 1.3 | 6.9 | tr | 0.0 | 0.0 |
| Snakes | 0.0 | 0.0 | 0.0 | 2.4 | 0.2 | tr | 4.3 | 0.4 | 0.7 | 8.6 | 0.9 | 6.2 | 0.0 | 0.0 | 0.0 |
| Lizards | 5.8 | 0.8 | 1.1 | 6.1 | 1.2 | 1.5 | 6.2 | 0.3 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Frogs | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 14.3 | 1.4 | 0.7 | 2.9 | tr | tr | 0.0 | 0.0 | 0.0 |
| Snails | 0.6 | tr | tr | 1.8 | tr | tr | 7.6 | 0.8 | 0.2 | 28.6 | 6.0 | 2.6 | 0.0 | 0.0 | 0.0 |
| Coleopt. | 76.9 | 27.9 | 12.2 | 92.1 | 40.5 | 17.6 | 85.6 | 37.9 | 13.2 | 100 | 78.6 | 45.8 | tr | tr | tr |
| Orthopt. | 32.0 | 4.2 | 1.8 | 35.4 | 2.4 | 1.0 | 38.3 | 7.3 | 2.0 | 10.0 | 0.6 | 0.3 | 0.0 | 0.0 | 0.0 |
| Arachnida | 0.6 | tr | tr | 1.8 | tr | tr | 5.7 | 0.4 | 0.1 | 5.7 | 0.30 | 0.1 | 0.0 | 0.0 | 0.0 |
| O. inver. | 1.9 | tr | tr | 4.9 | 0.3 | 0.2 | 0.5 | tr | tr | 5.7 | 0.3 | 0.1 | 0.0 | 0.0 | 0.0 |
| Fruits | 25.6 | 17.7 | 8.6 | 6.7 | 2.8 | 1.4 | 45.4 | 23.1 | 17.9 | 10.0 | 1.9 | 2.3 | 0.0 | 0.0 | 0.0 |

¹ Does not add up to 100 %.

[a] tr < 0.1.

To test whether the choice of MDQ affects guild assignment in an ubiquitous manner (i.e. it does not only occur in our Doñana assemblage), we considered six studies for which the diet of sympatric predators was quantified from samples of post-ingested remains using two methods. For each study, the taxonomic level of prey classification used was the same in both diet estimations and for all predators; thus, its effects on guild recognition and assignment (Greene & Jaksic, 1983) were controlled. The studies were: 1) Temblor Range (California, USA), where Leach & Frazier (1953) reported diets of mammalian carnivores, five of which where used in our analyses; 2) Larimer and Weld Counties (Colorado, USA), where Marti (1974) reported the diet of four sympatric strigiformes; 3) Amherst Island (Ontario, Canada), where Phelan & Robertson (1978) documented the diet of three falconiformes and three strigiformes; 4) Bialowieza National Park (Poland), where five mammalian carnivores were studied by Reig & Jedrzejewski (1988); 5) Biosphere Reserve of La Michilia (Durango, Mexico), where the diet of six falconiformes was studied by Hiraldo *et al.* (1991); and 6) Snake River Birds of Prey Area (Idaho, USA), where a predator assemblage comprising two mammalian carnivores, six strigiformes, six falconiformes, one raven and two snakes was documented by Marti *et al.* (1993).

## RESULTS

Considering dissimilarity matrices from the carnivore assemblage of Doñana, Mantel's permutation test indicated that the regression coefficient for the relationship FO-DWP (R = 0.887) differed significantly from zero (Table II). In contrast, the regression coefficient of DWP-FBI (R = 0.639) and FO-FBI (R = 0.297) did not differ from zero (Table II). These results indicated that although FO and DWP methods yielded close patterns of dissimilarity, DWP-FBI and FO-FBI did not. As expected, cluster analyses based on the FO method distinguished the rabbit-eating Iberian lynx, with all other carnivores assigned into an insect feeding guild (Fig. 1a; Table I). With this quantification method, the presence of prey weighing 1 g (i.e., Coleoptera) has the same importance as the presence of prey weighing 800 g (i.e., lagomorphs). Because the DWP method partly corrects this fact, cluster analyses based on this method assigned both foxes and badger in scrubland together in an omnivore guild (Fig. 1b), whose diet was based on lagomorphs, coleopterons and fruit (Table I). Although badger in pastureland was set apart in the insect feeding guild because of a diet based on Coleoptera, the Iberian lynx remained in the rabbit-eating guild. Cluster analysis based on the FBI method produced contrasting guild affiliations, assigning lynx, both fox and badger in scrubland to the rabbit-eating guild (Fig. 1c), whereas badger in pastureland remained isolated in the insect feeding guild due to its high biomass consumption of Coleoptera (see Table I).

Results based on other assemblages corroborated conclusions from Doñana. Dissimilarity matrices showed significant association in only three out of five comparisons (Table II), although a simple meta-analysis of results (p-values) suggested that overall regression coefficients were significant (Fisher Test for Combining Probabilities, $\chi^2 = 30.48$, df = 10, p < 0.001). In four assemblages there were changes in the number of guilds, depending on MDQ. Changes in guildmate affiliations characterized all assemblages. Mean percentage guildmate fidelity (GMF) was only 30 % (1SD = ± 21, n = 6), and ranged from 0 to 54 %
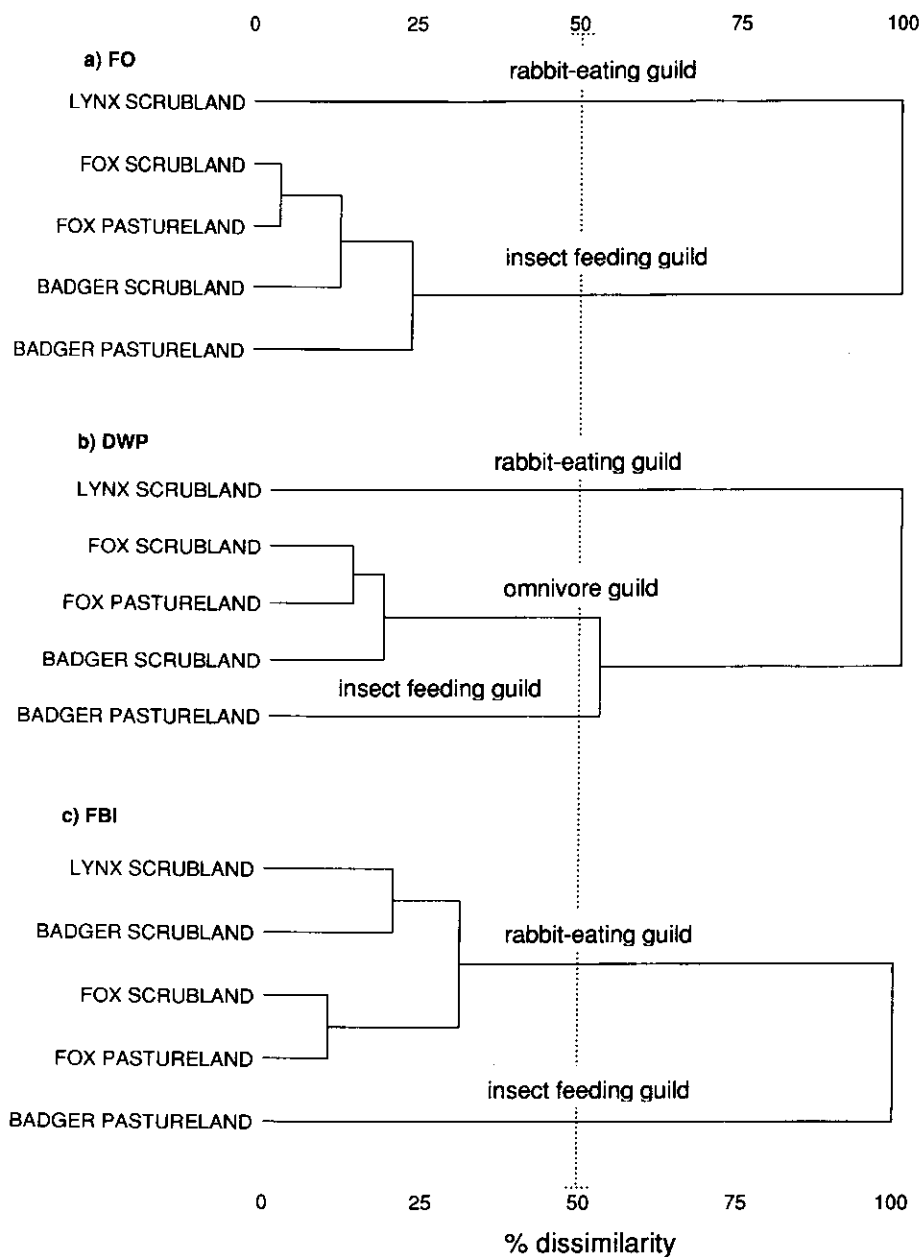
Figure 1. — Clustering of the Doñana carnivores studied by means of three diet quantification methods. Note that dendrograms 'a' and 'b' are rather coincident, but not others comparisons. Cophenetic correlation indexes were 0.95 for frequency of occurrence method (FO), 0.75 for dry weight of prey remains method (DWP), and 0.92 for fresh biomass ingested method (FBI).

TABLE II

*Changes in diet dissimilarity, number of guilds recognized and guild membership fidelity at 50 % dissimilarity, using different methods of diet quantification (MDQ) for the seven predator assemblages studied. R = regression coefficient for the relationship between each pair of diet dissimilarity matrices. p = probability that the regression coefficient differs significantly from zero. I) Methods based on prey occurrences. II) Methods based on prey numbers. III) Methods based on volume or dry weight of prey remains. IV) Estimates of fresh biomass ingested. Percent of guildmate fidelity (%GMF) = (number of pairs of guildmates matching in both phenograms compared) × 100 / (number of pairs of guildmates matching plus those not matching in both phenograms (N)).*

| R | p | No. of guilds recognized by different MDQs | | | | %GMF (N) | Source |
|---|---|---|---|---|---|---|---|
| | | I | II | III | IV | | |
| 0.762 | 0.008 | — | 4[b] | 4[c] | — | 0 (2) | Leach & Frazier (1953) |
| —[1] | — | — | 2[b] | — | 3[e] | 33 (3) | Marti (1974) |
| 0.381 | 0.171 | — | 3[b] | — | 2[c] | 27 (11) | Phelan & Robertson (1978) |
| 0.917 | 0.018 | 3[a] | — | — | 4[f] | 50 (2) | Reig & Jedrzejewski (1988) |
| 0.625 | 0.044 | — | 4[b] | — | 3[e] | 14 (7) | Hiraldo et al. (1991) |
| 0.090 | 0.209 | — | 2[b] | — | 2[c] | 54 (130) | Marti et al. (1993) |
| 0.887 | 0.008 | 2[a] | — | 3[d] | — | 50 (6) | This study |
| 0.639 | 0.126 | — | — | 3[d] | 2[f] | 50 (6) | This study |
| 0.297 | 0.228 | 2[a] | — | — | 2[f] | 33 (9) | This study |

[1] = matrix size too small for test. Detailed MDQ: [a] = number of feces containing each prey type × 100 / total number of feces. [b] = number of prey identified of each type × 100 / total number of prey identified. [c] = volume of remains of each prey type in stomach contents × 100 / total volume of prey remains. [d] = dry weight of remains of each prey type in feces × 100 / dry weight of total prey remains. [e] = number of each prey × its mean weight × 100 / $\Sigma$ (number of each prey × mean weight of each prey). [f] = dry weight of remains of a particular prey type in feces × its correction factors (CF) × 100 / $\Sigma$ (Dry weight of remains of each prey type × CF of each prey type).

(Table II). Because the arbitrary choice of 50 % of dissimilarity for defining guilds (though it facilitates comparisons), we also estimated guildmate fidelity at 25 % and 75 % of dissimilarity to assess if the guildmate shifts occur regardless of breakpoint. Values of GMF at those breakpoints of dissimilarity were in general low and variable [mean percentage GMF were 59 % (1SD = ± 33), and 64 % (1SD = ± 21), for 25 % and 75 % dissimilarity criteria, respectively].

## DISCUSSION

Issues other than MDQ may influence patterns of guild assignment (e.g., similarity index or clustering algorithm), thus caution devoted to the choice of MDQ should be also placed into those other issues. Nonetheless, differences between dendrograms due to MDQ, in contrast with potential inconsistencies due to other issues, can be interpreted in ecological terms since guilds identified by

different MDQ have differing conceptual connotations (see below). On the other hand, we applied the same protocol (a widely accepted one in feeding ecology of predators) to all data sets; thus, differences between dendrograms revealed the effects of MDQ, and these differences were not outcome of other issues.

Trophic guild recognition and assignment is highly sensitive to choice of MDQ. For instance, omnivorous predators such as the Red Fox, Eurasian Badger, Egyptian Mongoose (*Herpestes ichneumon*), Coyote (*Canis latrans*), American Badger (*Taxidea taxus*), Burrowing Owl (*Speotyto cunicularia*), Austral Pygmy Owl (*Glaucidium nanum*), and Common Raven (*Corvus corax*), all of which preyed on insects and mammals, were assigned to different guilds of insectivores when diets were quantified on the basis of prey numbers (cf. Jaksic & Delibes, 1987; Jaksic *et al.*, 1993; Marti *et al.*, 1993). But dietary analyses based on biomass, considered them to be carnivores (cf. Palomares & Delibes, 1991; Marti *et al.*, 1993; Silva *et al.*, 1995; Fedriani *et al.*, 1999). Moreover, shifts in guild membership do not arise in a predictable fashion, and consequently cannot be corrected in a standard fashion across data sets. For example, methods based on prey numbers yielded a number of guilds which was larger, smaller, or the same as that when using estimates of ingested biomass by predators (Table II).

Once we have shown that inconsistences in guild classification arrived as a consequence of MDQ in an ubiquitous manner, it is meaningful to discuss which MDQ should be chosen to identify guilds. Methods based on prey occurrences or numbers are easier to apply, and directly comparable with most other studies of predator diets (Corbett, 1989; Rosenberg & Cooper, 1990). However, trophic guild studies of predators based on occurrences or numbers of prey in the diet have been questioned (Simberloff & Dayan, 1991) since their estimates of predator diets are not always directly related to the nutritional or caloric importance of prey to the predator. On the other hand, methods that estimate the fresh biomass ingested by predators are more elaborated and time consuming and, frequently, more suscep-tible of bias (Rosenberg & Cooper, 1990; Ciucci *et al.*, 1996).

We propose that the choice of MDQ depends on the specific ecological question being addressed. One approach is to focus on the connections between predators and their prey as a mean of describing processes of energy flow and material cycling within an ecosystem (Paine, 1980; Pimm *et al.*, 1991). Biomass ingested is related closely to energy intake and may be an estimate of connection strength between guilds of predators and their prey; thus, it seems the best choice for this purpose. In addition, ecologists interested in guilds as the focal unit for detailed studies of interspecific competition (Winemiller & Polis, 1996) must consider effects of prey on predators, given that competition is likely to occur for a key resource (Wiens, 1989). Although a weak positive per capita effect of a small prey on a large predator is predicted by most theoretical models of food webs (Pimm, 1982; De Ruiter *et al.*, 1996; but see Abrams, 1992), large quantities of small prey may represent a significant amount of the nutritional or caloric intake of predators; therefore, both small and large prey can be a staple resource for predators and thus become object of food competition among them. Because estimates of ingested biomass are the only methods that weight prey numbers according to their mass by a meaningful biological unit (g eaten), we consider them the best choice when focusing on food competition.

The effects of predators on the abundance and dynamics of prey is also a critical issue in ecology. A negative per capita effect of predators on prey generally is predicted by theoretical models (Pimm, 1982; De Ruiter *et al.*, 1996; but see

Abrams, 1992). The strength of those effects depends on the fraction of prey population killed but this is unknown for most food webs because of logistic limitations (Winnemiller & Polis, 1996). Therefore, a metric closely related to that fraction but easier to estimate is needed. In contrast, top vertebrate predators may positively affect prey populations as a consequence of intraguild predation on intermediate predators (e.g., Crooks & Soule, 1999) through the "cascade effects" (Polis, 1994). Guilds of predators recognized on the basis of prey numbers may be the most appropriate approach to emphasize the degree to which groups of predators affect their prey. Conceptually, these feeding guilds defined on the basis of prey numbers in diets of predators would constitute "groups of functionally similar species" (Hawkins & MacMahon, 1989). Whether those direct and indirect effects produce subsequent changes in community structure and composition, allowing the construction of "functional food webs" (sensu Paine, 1980) is controversial and only resolvable by manipulative experiments.

Wildlife managers also may need accurate definition of predator guilds (Hawkins & MacMahon, 1989). For instance, functional redundancy (Walker, 1992) among vertebrate predators has been proposed as a useful criterion for making management decisions concerning biodiversity conservation (see Jaksic *et al.*, 1996). By the "redundancy strategy", conservation efforts should be focused on one species of each predator trophic guild. If managers attempt to conserve vertebrate predators because their "charismatic" or vulnerable nature, trophic guilds must be recognized on the basis of their staple prey, which are better represented in estimations of biomass ingested. But, if the ultimate goal is to preserve the "functional roles" of predators on prey, an approach based on prey numbers would be more adequate.

In conclusion, we have found that different MDQ lead to trophic guilds variable not only in predator species composition but also conceptually. Therefore, we support that, in agreement with Hawkins & MacMahon (1989), for these guilds "the usefulness of the concept depends more on the investigator's acuity and care than it does on the organism and their interaction in nature".

## ACKNOWLEDGEMENTS

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