

Describing food habits and predation: field methods and statistical considerations

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11.1 Quantifying predators' diets

During the last century, a variety of field techniques have been developed to gain insight into predator–prey relationships. A common starting point for a predator–prey study is to quantify the predators' diet. Although the analysis of diet reveals little of the predation process (an item being ingested through predation or scavenging), diet information helps us understand how predators of a particular species relate to their various potential prey and to their environment. Traditionally, diets have been analyzed using scats, stomach contents, by searching for kills of radio-collared individuals, and by following animals' tracks in the snow or sand. These methods are still important but have been supplemented by recent advances in DNA technology, such as DNA barcoding (Roth *et al.* 2007; Valentini *et al.* 2008) and stable isotope techniques (Crawford *et al.* 2008). These new techniques provide more certain identification of prey species in scat samples and avoid the many problems of visual or microscopic identification (Teerink 2004).

11.1.1 Scat analysis

Scat analysis is used widely to estimate the amounts of different foods ingested by carnivores based on identifying the indigestible parts of animals and plants found in scats (Putman 1984). Standard laboratory procedures (reviewed in Reynolds and Aebischer 1991) allow the identification of prey species from macroscopic, undigested remains, such as teeth, bones, feathers, tissues, and exoskeletons of insects, and from microscopic analysis of hair and of invertebrate exoskeletons found in scats. Items in scats can be identified using classification keys (Day 1966; Teerink

2004) and by comparison with reference materials (e.g. seeds, feathers, skeletons) collected from the study site. When analyzing scats of small- and medium-sized predators, examine also microscopic remains to ascertain the occurrence of chetae, as earthworms can comprise a substantial part of a diet.

Scat analysis is simple, cheap, noninvasive, allows relatively large sample sizes, but presents both technical and interpretation difficulties. Bias and sampling error can arise as early as during scat collection due to the inclusion of scats from non-target species, or due to inadequate study design. Collecting scats at kill sites, along predator tracks, or along trails is particularly prone to bias for predators with large prey because the production of several scats per individual prey may lead to over-representation of a given prey item. If such pseudoreplication occurs, subsampling is useful (Mattson *et al.* 1991), or considering all scats collected at a single kill-site or along one trail as one sample (Marucco *et al.* 2008). Modeling can help in finding the optimal sample size to avoid a lack of power when comparing diet within and among species. Targeted collection of scats is sometimes desired; scats at a den might provide insights into the diets of offspring vs. adults (Lindström 1994; Panzacchi *et al.* 2008a). In addition, recently developed fecal DNA methods allow sex determination from scats (e.g. Hedmark *et al.* 2004), potentially allowing one to compare diets by sex.

A second possible source of bias and error lies in the misclassification of food remains. Some predators ingest a wide variety of animal and plant items, as well as anthropogenic foods, such as garbage, whose remains in scats take the form of macroscopic fractions intermingled with microscopic particles. This bias and error can be reduced through proper training of the lab personnel (Spaulding *et al.* 2000) and by applying the point frame method for identifying prey remains (Ciucci *et al.* 2004). Even when prey remains are identified correctly, their ecological significance should be carefully considered. For instance, hairs of predators of the target species, which occur often in scats, might indicate intraspecific predation, or scavenging, or simply self-grooming. Similarly, it is not possible to conclude whether prey remains in a scat indicate predation or scavenging.

Choice of analytical method is critical. As no unbiased procedures exist, combining techniques is recommended. As an index of how often a predator eats a given prey item, the most simple and time-saving method is the *frequency of occurrence* (FO), which measures the number of scats (n_i) containing remains from food category i with respect to the total sample size of scats (N), thus (Leckie *et al.* 1998):

$$FO_i(\%) = (n_i/N) * 100.$$

Even though the FO has the advantage of providing results that can be compared among studies, it has the disadvantage of treating all prey items equally, regardless of size or probability of leaving remains. Hence, it over-represents small items such as insects (Ciucci *et al.* 1996).

A modified version of the frequency of occurrence, the *whole scat equivalents* (WSE), attempts to limit this problem by summarizing the relative volume or weight of each prey category within the sample (Angerbjörn *et al.* 1999). The plot of the FO against the mean volume, which can be calculated by dividing the sum of the volumes of each item in all scats by the total number of scats, helps one visualize the contribution of each item to the total volume of the scats (Kruuk and Parish 1981). Such methods based on volume are usually quick and easy, but they contribute little to understanding the amounts of different foods ingested or the nutritional value of the food.

If one wishes to investigate consumption or gain insight into the nutritional significance of different foods, combine FO with methods that use remains in the scats to estimate the fresh weights of different foods ingested. Methods based on biomass seem to have the greatest potential for estimating the actual bulk consumed, but they tend to be the most time-consuming, as accurate models describing the relationship between prey biomass consumed per scat produced are required (Rühe *et al.* 2008). The proportion of each macroscopic item can either be measured directly, or can be estimated by volume, and then multiplied by the total dry weight of the scat to estimate the dry weight of each food category (Reynolds and Aebischer 1991). Then apply coefficients of digestibility, quantifying the ratio of fresh weight of a given prey to the dry weight of its remains in scats, to estimate the fresh weight consumed (e.g. Jędrzejewski and Jędrzejewska 1992). Coefficients of digestibility can be obtained through rigorously repeated species-specific feeding trials, where predators are fed known amounts of different foods (Lockie 1958; Weaver 1993). The weights of consumed earthworms can be estimated from the number of chetae and gizzard rings (Brøseth *et al.* 1997). Even though coefficients of digestibility can be found in literature for some species, their definitions vary among authors and the combination of different coefficients may lead to significant biases (Reynolds and Aebischer 1991). Estimates of biomass ingested is overestimated using this approach, when the prey are not completely consumed (Ciucci *et al.* 1996).

As all methods for extrapolating from occurrence in feces to biomass or energy consumed are fraught with a range of errors and assumptions, researchers often adjust techniques to their particular studies, thereby producing countless variants of each technique and complicating comparative studies among species or areas. Nonetheless, all above-mentioned methodologies tend to rank prey items similarly

when the diet is based on few, large prey (Ciucci *et al.* 1996). Inconsistencies often arise, however, when the diets include a wide spectrum of prey sizes and species (Liberg 1982). Quantifying biases and errors associated with data collection and analysis (see Reynolds and Aebischer 1991) facilitates comparisons among studies.

11.1.2 Analysis of partly digested food items

If a sufficient number of carcasses of the target species are available (e.g. due to hunting or trapping), diet can be investigated by evaluating the contents of stomachs and gastrointestinal tracts (Thompson *et al.* 2009). The method is based on washing and separating the material contained in the gastrointestinal tract with a sieve, and identifying prey remains using classification keys and reference collections. As with scat analysis, FO should be complemented with methods providing estimates of the nutritional significance of foods to the predator. For each food item, multiply indices of metabolizable energy by estimates of the minimum and maximum food consumption per meal, obtained from captive conspecifics, to get estimates of caloric intake. This method accommodates different digestibilities among foods, and therefore accommodates the importance of large items.

An advantage of analysis of stomachs and gastrointestinal tracts is that the sex, age, and body condition of individual predators are usually available. One disadvantage of the investigation of the gut contents is that the results may not be comparable to those obtained with scat analysis; even the contents of stomachs and intestines may differ considerably (Witt 1980). Discrepancies in the outcomes of the three approaches reflect differences in the process of digestion at different stages. Of course, carcasses and scats may suffer different age and sex biases (Cavallini and Volpi 1995). If the carcasses belong to animals killed at bait, gut analyses should be avoided or the results should be interpreted with care.

11.1.3 Snow- and sandtracking

Following tracks in the snow has been an important source of data on predation in northern environments. Snow can be a good substrate to record animal tracks and often allows one to follow continuous behavioral sequences with little bias related to prey detectability. Sometimes one can assign a track to an age or sex class based on size and behavior (raised leg urination, for example, by canids). Following tracks allows a researcher to collect scats and document kills, to investigate hunting behavior (sometimes of known individual predators), and to quantify hunting success (Sand *et al.* 2005). Tracks can be used to monitor predator populations (Chapter 16), based on statistical modeling of track frequencies and distributions (Wabakken *et al.* 2001), or based indirectly on DNA analyses from scats collected

along tracks (Kohn and Wayne 1997). Sometimes one can estimate the age of the different stretches of track, facilitating the calculation of kill rates (Pedersen *et al.* 1999) and the predator's functional response (O'Donoghue *et al.* 1998). Snow-tracking combined with radio-telemetry (Chapter 7) improves the temporal precision of track data and identifies individuals leaving tracks. Sand may also provide a suitable substrate for following predator tracks (Bothma *et al.* 1984). The major drawback of ground-tracking methods is their dependence on weather and climatic conditions; for some studies, the difficulty of assigning tracks to individual predators is a problem.

11.1.4 Telemetry-based methods to study predator diet

The development of VHF radio-telemetry methods in the 1960s and 1970s allowed individual-based studies of animal movement and behavior. By using telemetry to locate a predator frequently and to document its movements, activity patterns, and habitat use, a researcher can identify potential kill-sites. Intensive aerial-tracking surveys within given time periods (e.g. Vucetich *et al.* 2002) can be effective but are expensive, constrained by daylight and good weather conditions, and often biased due to low detection rates of kills in closed habitats and during snow-free periods, especially for small prey species. Searches of potential kill-sites often produce prey remains. Because telemetry allows kills to be linked to time, one can calculate kill rates. Such methods remained the standard approach for studying large predators (e.g. O'Donoghue *et al.* 1998; Laundre 2008; Nilsen *et al.* 2009a) until the late 1990s. Data collected by this method may, however, be biased towards large prey items, which are easy to detect and which cause a predator to spend more time at a kill site or revisit the site several times. The use of carcass-searching dogs can reduce this bias. In the late 1990s, the advent of GPS technology provided many new opportunities (Chapter 7). GPS data are more accurate than traditional VHF telemetry data and typically allow the collection of many more location estimates (Sand *et al.* 2005). As a result, the detection of kill sites has improved immensely, producing more reliable measurements of kill rates, even under snow-free conditions when carcasses are hard to find. GPS telemetry has been used predominantly with large-bodied predators (>10 kg) that can carry the weight of a GPS collar and that consume mostly large prey (Figure 11.1).

With respect to studying predation with GPS telemetry, researchers need to develop objective criteria to identify points of interest, especially clusters of positions, to prioritize in an unbiased manner the sites for ground searches for prey remains. Researchers have started to develop rules for identifying kill sites (Anderson and Lindzey 2003; Sand *et al.* 2005; Zimmermann *et al.* 2007). Binomial regression models for presence and absence of large kills at clusters of GPS



Fig. 11.1 By visiting clusters from radio-collared animals, researchers are able to find the remains of prey animals. Top photo shows the remains of a hare (photo: Robert Needham), whereas the lower photo depicts the carcass from a semi-domestic reindeer (photo: Andrea Mosini). Both prey were located by visiting clusters of tracking positions from radio-collared lynx in Northern Norway.

positions (Anderson and Lindzey 2003; Zimmermann *et al.* 2007), two-step binomial and multinomial regression that estimate the probability of a site holding a large-bodied kill, a small-bodied kill, or no kill (Webb *et al.* 2008), classification trees that divide clusters into kills or non-kills by threshold criteria of predictor variables (Tambling *et al.* 2010), and hidden Markov modeling techniques to

distinguish kill sites, bed sites and movements (Franke *et al.* 2006), all hold potential. In multicarnivore systems with predator interference, field visits to clusters are needed to determine displacement and scavenging, which might bias estimates of kill rates based on cluster methods (Ruth *et al.* 2010). Sampling effort required appears to depend heavily on characteristics of both predator and prey; kill sites appear easier to find for large, solitary felids that hunt large prey than predators such as wolves that show less stereotypic behavior when handling kills. Several issues, such as positioning bias in different habitats, still require attention, yet this new technology is opening a range of possibilities that were inconceivable only 10 years ago. Telemetry-based approaches, however, are less useful for finding smaller prey items or multiple or surplus killing events (common for livestock) when the predator does not stop for a significant period to consume the item killed.

11.2 Ecological inferences from diet data

The field methods described above are much utilized techniques in many field studies of predator–prey interactions. However, with these data at hand, one might also ask questions that go beyond simply describing the diet and food habits of the predator—questions that directly relate to the impact of predation on the prey population. We will here focus on methods used to estimate kill rates and functional responses, prey selection, niche breadth, and diet overlap.

11.2.1 Quantifying kill rates and functional responses

Kill rate is defined as the number of prey items killed by a predator (individual or group) within a certain time window. Linking this information to prey density (Holling 1959) or predator and prey density (Abrams and Ginzburg 2000) makes it possible to estimate the functional response of the consumer. Kill rates can be assessed directly by tracking predators on snow or with telemetry during defined sampling intervals with the aim to detect all kills within these periods, can be assessed indirectly by comparing prey densities or mortalities in areas or time periods with and without predators, or can be inferred from scat analysis.

Estimating functional responses based on such field data is not trivial. Estimates of prey (and predator) density must be available (Chapter 5). Obtaining robust density estimates remains a challenge. When data are available to model functional responses, the most commonly used approach is to fit non-linear regression models to the data, assuming Gaussian distributed error terms, and to compare candidate models based on Akaike's information criterion (AIC) (Vucetich *et al.* 2002; Nilsen *et al.* 2009a). Robust model selection is often hampered, however, by the

need for large datasets to estimate key parameters in the models (Marshall and Boutin 1999; Nilsen *et al.* 2009a; see also Vucetich *et al.* 2002). If one assumes that prey depletion is negligible within the sampling period, as is usually assumed for large predator–large prey systems, models are usually expressed as kills per time unit (often per month or 100 days for large carnivores). Integrated models may work better when prey are depleted (Vucetich *et al.* 2002).

In addition to the challenge of differentiating among different functional responses, different sampling regimes can yield different estimates for the parameters in a particular functional response model. At Isle Royale, USA, comparing functional-response models for wolves preying on moose across different spatial scales (whole island, per pack, and “mixed scale”) resulted in different models being selected for different spatial scales (Jost *et al.* 2005); nonetheless, the selected models included predator dependence and satiation at all scales. Because the number of tracking days needed to obtain robust estimates of kill rates varies for different predator–prey pair systems, the number of tracking days should be included as a part of the general assessment of the robustness of the estimated model. New methods for analysis of GPS telemetry data are continuously being developed, for example, distinguishing between search time and handling time (Merrill *et al.* 2010) allowing researchers to test predictions of optimal foraging models. Search plus handling times sum to the inverse of kill rate. By relating search time to habitat variables and prey densities, attack success and predation risk can be assessed from environmental variables directly. For small predators, obtaining kill sequences by following individuals is complicated because (1) the remains of the kills are hard to find and recover, (2) the predators’ small body sizes result in rapid (often within a few minutes) and total consumption, and (3) some species, such as stoats (*Mustela erminea*) and weasels (*M. nivalis*), frequently kill prey in subnivean or subterranean spaces. Thus, inferences based on a predators’ diets have been used to estimate predator kill rates and functional responses (Gilg *et al.* 2003, 2006). The basic assumption in these approaches is that a close link exists between a predator’s diet and its functional response, so that the relative occurrence of a given prey in the predator’s feces, together with knowledge of the predator’s metabolism, can be used to calculate prey consumption. In an alternate approach, Sundell *et al.* (2000) manipulated the densities of radio-collared voles (*Microtus*) within large enclosures, measured kill rates of weasels at different prey densities in a relatively controlled manner, and thereby estimated a functional response.

Miller *et al.* (2006) inferred about predator functional responses from variation in observed survival rates of prey by integrating formulations of predator functional responses into the estimator of survival. This approach opens the possibility of using data on prey survival to estimate directly one of the key parameters of a

predator–prey system. Advances in the modelling of survival probabilities might prove to be a valuable extension to analysis of functional responses, at least in cases where mortality factors are known and mainly caused by predation.

The final aim of diet analysis is often to estimate the total consumption by a predator population. Differences in diet among groups of scats (e.g. collected from animals in different areas or in different seasons) can be detected using χ^2 tests or contingency tables (Wright 2010), or with logistic regression to model the presence or absence of a given item in the scats. Multinomial models developed for capture–mark–recapture data can be used to quantify uncertainty of diet estimates and to assess differences in diet composition when using presence/absence data (Lemons *et al.* 2010). The capture–mark–recapture approach should be more productive when foods are quantified by weight or volume. As the proportions of different food items in a scat are interdependent (i.e. they sum up to one), such data should be analyzed with methods taking into account this interdependency (e.g. compositional data analysis; Reynolds and Aebisher 1991; Aitchinson 1986).

11.2.2 Studying selection—the difference between use and availability

The basis for selection of prey is that individuals of different species, or subgroups within species, yield more energy than do other prey (Krebs and Davies 1993). One generally expects a predator always to try to capture the energetically most valuable prey if encountered, whereas other prey should be captured only if the most valuable prey is rare (Charnov 1976a, 1976b). Apart from experimental work, direct tests of this hypothesis are uncommon, as estimating energy yield and expenditure associated with different prey items is not easy.

Technically, prey selection is a measure of the deviance between the proportion of prey X in the diet, compared to the availability of prey X in the standing population of all prey. Study designs for measuring used and available are grouped into three main categories based on the definitions and assumptions regarding use and availability (Manly *et al.* 2002). In Design I, the resource (prey) use is not recorded for specific individuals, and used and available resources are assumed to apply to the whole predator population in a study area. Individual resource use is recorded in the Designs II and III. For Design II, the availability of resources is estimated at the population level but for Design III the availability of resources is estimated at the individual level. Sampling of scats usually allows only the application of Design I. Since the introduction of fecal genotyping, however, scat analyses may also convey individual-based information, thus allowing use of Design II (Prugh *et al.* 2008). Design III can be applied in telemetry-based studies, if estimates of prey availability are available for each individual predator. Among the three categories of study designs, Designs II and III clearly have the potential to

address a wider range of questions. For instance, variation in prey selection with respect to sex and age classes cannot be analyzed using Design I. Taking individual differences into account provides insights into patterns of resource partitioning stemming from individual specialization (Araújo *et al.* 2010), which may have stabilizing effects on population dynamics (Kendall and Fox 2002) and may affect sympatric speciation (Schluter and McPhail 1992).

A common difficulty in all studies of prey selection is defining and estimating prey availability. Prey availability is not directly equivalent to prey abundance (Molinari-Jobin *et al.* 2004). Rather, prey availability is a function of prey abundance, prey antipredator behavior, differential vulnerability of prey of different life-cycle stages, and more. Consequently, prey availability changes across time, not only because prey abundance changes, but also because different age classes are more prone to predation. Prey vulnerability might change regionally (Molinari-Jobin *et al.* 2004; Panzacchi *et al.* 2008b; Nilsen *et al.* 2009b).

Once use and availability of prey have been estimated, several methods exist to measure selection. Manly's selection index compares the relative usage (r_i/n_i) of prey of category i (species, age class or other categorical variables) to the relative usage of all prey $\sum r_j/n_j$ in the environment; Chesson 1978):

$$\alpha_i = \frac{r_i/n_i}{\sum r_j/n_j},$$

where r_j represents the resource of category i that is used, n_i the resource in category i that is available the selection index α_i range from 0 to 1, and a higher value indicates greater selection.

Estimates of both use and availability of prey are susceptible to biases and error that increase the risk of rejecting the null hypothesis of no selection (Type I error). Furthermore, values of Manly's index depend strongly upon which prey species are considered to be available. Including or not including an abundant prey species that is rarely consumed may reverse preference classifications of the other prey species (Johnson 1980). In such cases, using Johnson's (1980) rank index is less sensitive to subjective choices of available resources. This index ranks use and availability of resources and the difference in ranks forms the basis of selection classifications.

In the literature, *use*, *selection*, and *preference* are often applied interchangeably. Use and preference generally differ from selection by being independent of availability. Use refers to a food item being consumed in a specified time period, while preference is the probability that a food item is selected when offered on an equal basis with other items. Accordingly, the existence of a preference requires an

outcome of behavior by the predator, whereas the selection index is simply an estimate of non-random association between predators and prey. Selection is not equivalent to importance. A prey type can be highly selected, even if it is relatively rare and, therefore, rarely eaten; accordingly, the importance of this prey for the survival and reproduction of the predator may be minimal compared to common prey that are not selected.

11.2.3 Quantifying food niche breadth and diet overlap

Diet data can be used to investigate and compare the diet breadth in different areas and periods and among different species. Based on the breadth of their diets in different ecological settings, focal species can be placed along the generalist–specialist continuum (Jedrezejewska and Jedrezejewski 1998). This approach also provides insights into the ways that species within ecological communities partition the available resources, and allows inferences on competition and coexistence.

The study of resource partitioning has a long history in community ecology. The term *trophic niche* was coined at the beginning of the twentieth century to describe the position of a given species in the foodweb of a community. In the absence of competition, the observed resource use constitutes a species' *fundamental trophic niche*, while in the presence of competitors the species' niche can be substantially different and it is termed its *realized trophic niche* (Hutchinson 1953). The breadth of the fundamental and realized trophic niches can be measured by a variety of classical diversity indices that are sensitive to both the number of items in the sample and to their relative abundance. One of the most widely used indices for measuring the niche breadth is the *Shannon–Wiener index* (H') (Krebs 1999):

$$H' = -\sum p_i(\ln p_i).$$

where p_i is the proportion of each food item in the sample. H' ranges from 0 (lowest niche breadth) to 1 (greatest breadth).

Alternatively, several studies use the *Levins' index*, B , and the *Levins' standardized index* B_s (Levins 1968):

$$B = 1/\sum p_i^2.$$

where p_i is the proportion of each food item in the sample;

$$B_s = B - 1/n - 1.$$

where n is the total number of food categories identified.

Both the choice of the method for quantifying the diet and the choice of the index for estimating the niche breadth affect one's results. While H' tends to

overestimate the importance of rare food items, B tends to emphasize the evenness in the distribution of items (Pielou 1975).

The first method for estimating niche overlap is based on the relative use of different segments of a niche resource axis and on the overlap between species in their use of common segments (MacArthur and Levins 1967). A variety of other indices followed (e.g. Schoener 1971) but one of the most widely used is the index of trophic niche overlap between species j and k developed by Pianka (1974):

$$O_{jk} = \sum p_{ij}p_{ik} / \left(\sum p_{ij}^2 \sum p_{ik}^2 \right)^{\frac{1}{2}}$$

where p_{ij} is the proportion of the food item i in the diet of species j . O ranges between 0 (total niche separation) and 1 (total overlap).

Multivariate ordination techniques, such as correspondence analysis, can be used for a graphical visualization of the resource partitioning in the community by displaying the matrix formed species (e.g. predator guild) and food items (e.g. prey guild) in a multidimensional space.

The indices of niche overlap provide useful insights into the resource partitioning within a community at a given time and place. Trophic interactions are spatially and temporally dynamic, however, and food niches converge and diverge as the diversity of resources changes (Schoener 1982). Hence, a repetition of a study in different seasons is often advisable. Also, the existence of trophic niche overlap does not necessarily imply the occurrence of competition, as competition is shaped by a variety of environmental and behavioral parameters (Colwell and Futuyma 1971).

11.3 Using stable isotopes to infer trophic interactions

Stable isotopes, particularly (but not only) those of carbon and nitrogen, can be used to investigate the assimilated diets of organisms and, hence, trophic interactions (Kelly 2000; Post 2002; Newsome *et al.* 2007). Foods vary systematically in their proportions of elemental isotopes: in the case of carbon, ^{12}C and ^{13}C , and for nitrogen, ^{14}N and ^{15}N (Brand 1996). The isotopic “signature” of a consumer’s tissues reflects the proportional intake of the isotopes in its diet (DeNiro and Epstein 1978), with correction for preferential uptake and loss of given isotopes in digestion process, known as diet-tissue or trophic fractionation. Trophic fractionation varies for different elements, species, and tissues (Dalerum and Angerbjörn 2005). Marine food-chains tend to be longer than terrestrial chains and baseline $\delta^{13}\text{C}$ values differ. Thus, when a predator mixes marine and terrestrial food

sources, the typically large differences in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ make discriminating their proportions in the diet relatively simple (e.g. Ben-David *et al.* 1997).

Using stable isotopes to estimate trophic position relies on trophic fractionation. Generally, $\delta^{15}\text{N}$ fractionates much more strongly than $\delta^{13}\text{C}$. Generic values for trophic fractionation, typically *ca* +3–3.4‰ for $\delta^{15}\text{N}$ and *ca* +1‰ for $\delta^{13}\text{C}$ (Kelly 2000; Post 2002), are often used in trophic analyses, but naive application of such values can be a pitfall for the unwary. The isotopic signature of a predator is not usually sufficient to infer trophic position without an appropriate isotopic baseline, and estimates of trophic position are very sensitive to assumptions about the trophic fractionation of $\delta^{15}\text{N}$ in particular, and to different methods of generating an isotopic baseline (Post 2002). The average $\delta^{15}\text{N}$ value for terrestrial omnivores in the literature is slightly *lower* than that for terrestrial herbivores, probably because of the very high fractionation values reported for ruminant herbivores (Darr and Hewitt 2008) compared to animals with simpler digestive processes. Moreover, different species eating identical diets vary up to 3.6‰ in $\delta^{15}\text{N}$ fractionation of the same tissue, i.e. more than a whole trophic level at the usual generic rate (Sponheimer *et al.* 2003). Therefore to conclude, without species- and tissue-specific fractionation being taken into account, that similar $\delta^{15}\text{N}$ values in different species of predator (or any animal) indicate trophically similar diets is unwise; or, conversely, that differences in values between species imply a difference in diet or trophic position.

This consideration also renders assessing variation in trophic niches of individual predators within a species more complex than simply reading off a $\delta^{15}\text{N}$ value and mapping directly to “trophic level.” Although for a given species and tissue, trophic fractionation can be assumed to be uniform in strict carnivores, whose foods are typically similar in protein concentration, uniformity may not be the case for omnivores, such as bears (Phillips and Koch 2002). Different prey species with identical diets may vary in isotope profiles, and prey of differing diets and trophic positions may have similar isotope profiles.

Where (1) baseline isotope values for diet sources (different prey species and isotopically distinct classes within those species) and (2) fractionation values for the predator tissue analyzed are fairly securely known or can be inferred, the comparison of stable isotope values within and among species is a powerful technique for assessing relative trophic niches and trophic niche width (Bearhop *et al.* 2004). A variation of this technique with wide application in predator studies is to use the method to assess the diet at different time periods, either by measuring tissues, such as blood plasma, with very rapid turnover, or tissues that capture the isotopic signature when growing but are thereafter metabolically inert, e.g. hair or horn (Dalerum and Angerbjörn 2005).

11.4 Estimating non-lethal effects of predation

Measuring the effects of carnivores on their prey is often limited to estimating the impact from the killing and consumption of prey (numerical or direct effects), as this is the most obvious effect of carnivores. Carnivores also affect prey survival, growth, and reproduction indirectly by altering prey behavior or physiology (risk effects or non-consumptive effects). In some cases, the risk of predation alone can be the strongest driver of population dynamics, even stronger than the direct effect of predation (Pangle *et al.* 2007). Because of this, risk effects can cascade to lower trophic levels through two pathways (Figure 11.2). For example, the presence of a carnivore can reduce the foraging time of an herbivore releasing local vegetation from both the reduction in herbivore foraging effort (*trait-mediated indirect effect*) and the reduction in herbivore numbers due to the nutritional costs of this antipredator behavior (*density-mediated indirect effect*). Understanding how carnivores shape the risk of predation as perceived by their prey is central to understanding ecosystem function.

Much of our understanding of risk effects comes from experiments with invertebrates and small animals (Preisser *et al.* 2005); yet much of this work has parallels with vertebrate carnivores in natural systems. Most prey animals are capable of detecting carnivores long before an attack and most prey possess several traits for avoiding predation. While physiological stress responses may exist (Boonstra *et al.* 1998), most research has focused on estimating behavioral responses and their costs. Common behavioral responses to the presence of predators are shifts in habitat selection foraging behavior and vigilance (Lima 1998). Although these responses correlate with one another, antipredator responses cannot be assumed to increase with levels of predation risk (McNamara and Houston 1987; Lima and Bednekoff 1999). Unfortunately, we have few examples where the demographic costs of behavioral responses to carnivores have been estimated for any wild prey species. Surprisingly, most research on risk effects with terrestrial carnivores has focused on estimating how changes in prey behavior affect lower trophic levels (e.g. hardwood plant regeneration in Yellowstone National Park following wolf recolonization; Fortin *et al.* 2005). We know little about how carnivores disrupt survival, reproduction, and growth in prey through risk effects (but see Creel *et al.* 2007).

Information on carnivore behavior is crucial to detecting and quantifying relevant antipredator responses in natural systems. Current approaches differ primarily in temporal and spatial scales. A dichotomous index of predation risk can be applied across the sampling space (carnivore-absent and carnivore-present). At the broadest scales, prey behavior, prey nutrition, or the dynamics of lower trophic levels are compared between ecosystems with and without carnivores

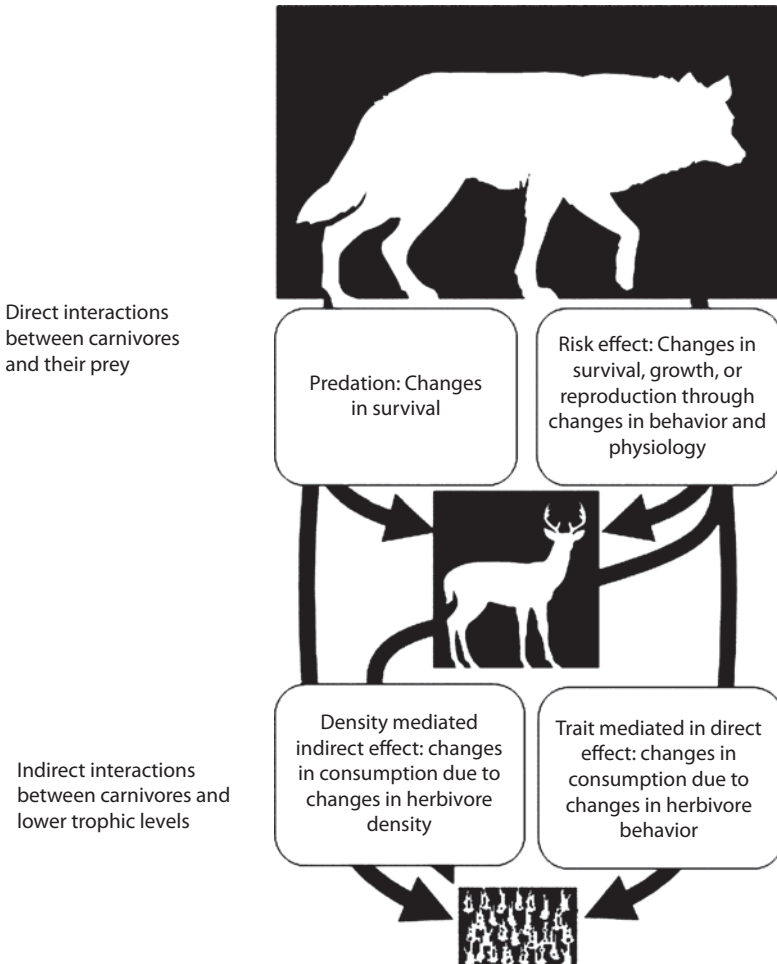


Fig. 11.2 Measuring the total impact of carnivores on ecosystems requires an understanding of the complexity of their interactions. For example, with three species at different trophic levels a carnivore should be expected to affect the demography of its prey through predation and by eliciting the expression of costly antipredator behavior in prey. Lower trophic levels might experience reduced grazing pressure if herbivore numbers are limited by predation, limited by the costs of antipredator behavior, or if herbivore foraging behavior is depressed as part of the antipredator response.

(Wolff and Van Horn 2003), sometimes with the use of predator exclosures (Hodges and Sinclair 2003). Similarly, prey behavior, prey nutrition, or plant dynamics can be compared within an ecosystem but over different states of carnivore status, e.g. prior to, and after, a reintroduction (Mao *et al.* 2005) or before, and after, predator removal programs (Banks *et al.* 1999). At finer scales,

particular groups of prey animals within one population or particular sites within a study system may be classified as under the influence of carnivores or not, and compared, e.g. groups near or far from refuges (Frid 1997). These latter methods have detected general relationships between carnivores, prey, and lower trophic levels. Nonetheless, these methods can mask the effects of predators if ecosystems differ widely over space and time. Moreover, many responses to carnivores often occur at fine spatial and temporal scales (Winnie and Creel 2007), indicating that most prey can distinguish variation in predation risk at much finer scales than are usually measured. Hence, the magnitude of the indirect effect of a carnivore could be underestimated or missed entirely at broader scales.

Information on local carnivores can provide finer spatial and temporal resolution of predation risk. Describing gradients of risk rather than dichotomies, such as estimating the carnivore/prey ratio over time and space (Creel *et al.* 2007) or describing spatial variation in local carnivore habitat use (Valeix *et al.* 2009), are becoming more common. These methods rely on efficient carnivore detection and tracking, such as snowtracking, radio-telemetry, or GPS collars.

Most current approaches for estimating the impact of predation risk from carnivores on ecosystems largely assume that a carnivore's proximity to a prey animal confers risk, and that the behavior of a prey animal in the presence of a carnivore reflects its efforts to increase its probability of surviving an attack. Nonetheless, some studies have shown that the behavior of a carnivore (beyond its movement) may also influence how prey determine risk. For example, wolves close to elk affect vigilance of elk, but how recently wolves have made a kill also matters (Liley and Creel 2008). Future research will likely reveal that prey animals are highly attuned to the behavior of local carnivores and adjust their antipredator behavior in response to changes of predation risk at very fine spatial and temporal scales. If so, quantifying the indirect effects of carnivores on ecosystems may require fine scale information on carnivore behavior coupled in time and space to the behavior of prey.

11.5 Some further challenges

While we have learned much about predator–prey dynamics, central aspects of predator–prey interactions are still understudied. Some of these aspects can be addressed using the field methods described in this chapter, other aspects require innovative thinking in the field. In a dynamic predator–prey system, a link between predator consumption rate and predator recruitment, and thus population growth, is generally assumed. Although several studies have documented a positive relationship between prey density and predator density (e.g. Carbone and

Gittleman 2002) and from this inferred a numerical response (Gilg et al., 2003), very few studies have been able to measure the relationship between predator consumption rate and predator population growth rate (Millon and Bretagnolle 2008; but see Vucetich and Peterson 2004). Gaining a better understanding of this relationship will greatly enhance our understanding of predator–prey dynamics. In addition, our knowledge of scramble competition and predator population growth is still very limited. Indeed, models of predator–prey dynamics may make assumptions that contradict behavioral models. For instance, while the hypothesis of economy of resource defense (i.e., territoriality) predicts that at very high and very low prey densities it does not pay to be territorial, many models of predator–prey dynamics assumes that predator interference limits predator number also when per capita food abundance is high. Compared to prey species, the demography and population dynamics of predators are understudied.

In a real and complex world, interactions between prey and predators are indeed complex. The context in which trophic interactions take place contributes to the outcome. We should, therefore, in the future not ask questions such as, “does predation affect prey population dynamics?” but rather seek to identify conditions that determine the relative strength of top-down and bottom-up effects. In some cases, these conditions might relate to the biotic aspects of the system, such as taxonomic differences, differences between hunting styles, and predator–prey body weight ratios, while they might also relate to factors describing the physical environment, such as terrain, landscape productivity, and climate. Further work is needed to integrate the field methods described in this chapter with conceptual models of how predator–prey system ought to behave under these various conditions.