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Food Habits

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INTRODUCTION

Wildlife managers first became interested in raptor food habits in their attempts to assess the impact of raptors on game animals and livestock (Fisher 1893, Errington 1930), but ecologists soon found other reasons to understand raptor diets. What a raptor eats, and how, when, and where it obtains its food not only are significant in understanding the ecological relationships of the raptor itself, but also for understanding community ecology. Besides helping researchers understand raptor niches and how they relate to community structure, studying raptor diets can provide valuable information on prey distribution, abundance, behavior, and vulnerability (Johnson 1981, Johnsgard 1990, 2002; del Hoyo et al. 1994, 1999). The debate on whether raptors can limit the densities of their prey continues today; Valkama et al. (2005) provided a comprehensive review of the literature on this topic with an emphasis on Europe that also includes an overview of North America.

In this chapter we present methods of analyzing and interpreting raptor diets and discuss related precautions, advantages and disadvantages, and biases. We present analytical techniques for the collection of prey in raptor diets including pellet analysis, stomach-content analysis, examination of uneaten prey in nests, direct and photographic observation of prey delivered to nests, and confinement of nestling raptors in order to prolong data-collection intervals. Procedures for identifying prey and interpreting and characterizing raptor diets through dietary diversity, rarefaction, prey-weight, dietary-overlap, and stable-isotope techniques are demonstrated as well as guidelines for assessing adequate sample sizes. Methods for evaluating the composition, density, and vulnerability of prey populations are closely related to studies of raptor food habits, but are beyond the scope of this chapter. See Fitzner et al. (1977), Otis et al. (1978), Burnham et al. (1980), Schemnitz (1980), Call (1981), Johnson (1981), Hutto (1990), and Valkama et al. (2005) for an entry into this literature. Also valuable to the subject of this chapter are bibliographies containing references to the foods of raptors. Olendorff and Olendorff (1968), Earhart and Johnson (1970), Clark et al. (1978), Sherrod (1978), Pardinas and Cirignolli (2002), and Valkama et al. (2005) provide a wide range of such information.

ANALYTICAL PROCEDURES

Below we discuss the advantages and disadvantages of

each technique as a guide to its selection for a particular question. Regardless of the method selected, sampling is a very important consideration in food-habits studies; inadequate samples can produce misleading conclusions (Errington 1932). Information should be collected from more than one bird, nest, and, depending on the study objectives, more than one season or year (Korpimäki et al. 1994). Non-representative food-habits data may be obtained if the sample size is too small, if a prey species is locally or temporarily abundant (e.g., during a population irruption), or if an individual or pair specializes on certain prey (i.e., behaves idiosyncratically).

Despite its importance, determining the adequate sample size prior to beginning a study may be difficult. Valid descriptions of diets that have a high variability in prey require more and larger samples than descriptions of diets with homogeneity of prey. Studies of seasonal changes in diet and inter- or intra-population dietary variation also require more samples. Investigators must ask whether it is important to document even those prey species eaten in very small proportions of the diet or whether it is more important to know which species are the mainstays of the raptor's diet, either numerically or by biomass. The answers to these questions will depend upon study objectives. See Morrison (1988) and Gotelli and Colwell (2001) and below for discussions on quantifying, evaluating, and justifying the size and nature of data sets, and Eckblad (1991) for general help on determining how many samples must be taken in biological studies, and our simulations included below relating sample size with dietary diversity and richness. Other statistical considerations are vital as well, and are similar to those in most biological situations (Sokal and Rohlf 1995).

Regurgitated Pellet Analysis

Most raptors, the Osprey (*Pandion haliaetus*) being a notable exception, produce pellets consisting of the less digestible remains of their prey including bones, teeth, scales, hair, feathers, keratin, and chitin. These materials are compacted by the stomach and regurgitated, usually daily. Identification of remains in pellets can provide both qualitative and quantitative information about the diet of a raptor. Although this method has been used for more than a century (Fisher 1893), Errington's (1930, 1932) extensive studies on raptor feeding did much to promote its use. Some early critics dismissed the technique of pellet analysis entirely (Brooks 1929), but it is now widely accepted as valid for most species. In general, pellet analysis is most reliable for owls (Errington 1932, Glading et al. 1943), and is generally less reliable for falconiforms because many of the latter species dismember prey prior to swallowing and may not ingest all portions (Craighead and Craighead 1956, Cade 1982). Falconiforms also digest bone to a greater extent than do owls (Duke et al. 1975, Cummings et al. 1976). Owls tend to swallow prey whole or in large portions, with less rejection of identifiable remains (Errington 1932, Duke et al. 1975). Errington (1932) believed that only young owls digested bones significantly, but Raczynski and Ruprecht (1974) and Lowe (1980) reported considerable bone loss attributed to digestion in adults; neither study, however, provided enough details on the analytical procedures to allow evaluation of accuracy. Others have reported that not all food fed to captive owls was represented in pellets (Errington 1932, Glading et al. 1943, Southern 1969). Nevertheless, Mikkola (1983) found very close correlation between food eaten and remains in pellets, and Duke et al. (1975) and Cummings et al. (1976) indicated that very little, if any, bone digestion occurs in owls.

Insectivorous raptors present a different problem. Even though the entire prey is usually swallowed, chitinous portions may be broken into small fragments that are difficult to identify. Chitin digestion, however, appears to be slight at least in American Kestrels (*Falco sparverius*) and Eastern Screech Owls (*Megascops asio*) (Akaki and Duke 1999).

Pellets containing remains of prey too large for a single meal (e.g., rabbits or hares eaten by eagles, large buteos, or owls in the genus *Bubo*) pose a problem of quantification. Did the raptor feed once on a large prey item and leave a portion, with the result that remains in a pellet represent only a part of the prey? Or, did the raptor return later and consume the rest, so that all or most of the identifiable remains are in several pellets? Evidence shows that some raptors do return to large kills for several meals (Bowles 1916, Brown and Amadon 1968), but the number of larger prey species eaten may be greatly underestimated when pellet analysis alone is used to determine food habits. Large prey items brought to nestlings have a greater chance of being consumed totally. The remains may be distributed in pellets of several siblings and, in some cases, those of the adults as well (Bond 1936, Collopy 1983a).

The most profitable strategy for collecting pellets is to search nest sites and roosts. Larger samples can be obtained, species of raptor verified, and seasonal or yearly trends in prey consumption both determined

from serial collections at the same site. Accumulation of data by this method is not uniformly successful with all raptors. Some species remain at one roost for long periods (e.g., Barn Owl [*Tyto alba*] and Long-eared Owl [*Asio otus*]), facilitating the collection of a large number of pellets (Marks and Marti 1984). However, many other species regurgitate their pellets over wide areas (e.g., Northern Harrier [*Circus cyaneus*] and Short-eared Owl [*A. flammeus*]), making collection of an adequate sample difficult (Errington 1932, Craighead and Craighead 1956, Southern 1969, Ziesemer 1981). It is important for statistical testing to collect pellets at as many nests, roosts, or both as possible to reduce problems associated with the lack of independent sampling.

Pellets of some species are distinctive in size and shape, but many are not. Guides to pellet identification for owl species are available (Wilson 1938, Burton 1984), but no method is foolproof for separating pellets of different species by appearance alone. To ensure that pellets are identified to species, only fresh pellets should be collected at nests, roosts, and perches known to be occupied by the raptor under study. The same nest sites often are used by different species at different times, so all old material should be removed and discarded prior to collecting new pellets for study.

Food-habits data are most valuable when the approximate date of deposition is known; hence, the knowledge of how long pellets persist in the wild is important. Moisture, invertebrates, and fungi rapidly break down pellets in exposed situations (Philips and Dindall 1979); most pellets in open environments decompose in less than 1 year (Wilson 1938, Fairley 1967, Marti 1974). In protected places, such as cavities, caves, or buildings, they may last much longer. Experiments to determine the rate of pellet decay in the local area of study might be necessary if there is doubt about how long pellets persist.

The method selected for pellet dissection depends upon the number of pellets to be analyzed and the objectives of the analysis. If the quantity is small or if the objective is to obtain immediate practical management information (e.g., to determine the principal food of a raptor or its impact upon a certain species of prey), pellets may be dissected individually by hand. Hair and feathers are teased away from bones, teeth, and other identifiable remains. Forceps and a dissecting needle are helpful aids for this. If quantities of pellets are large, or if better resolution of diet is required, hard remains should be separated from hair and feathers more carefully. This can be done by soaking and washing pellets with water. A more effective technique is to dissolve hair and feathers with sodium hydroxide (Schueler 1972). A modification of this procedure works well: dissolve 100 ml of NaOH crystals in 1 l of water, and then combine a sample of pellets with two to three times as much of this solution by volume. Two to four hours of soaking with occasional gentle stirring will sufficiently dissolve hair so that washing the solution through a screen (1/4 in mesh [6.35 mm]) will completely free the bones. Washing should be done over a pan to catch any fragments that pass through the screen, and the residue can then be washed, decanted, and added to the sample. Even very small, delicate bones are unharmed by this process, and the likelihood of finding smaller fragments is much greater than with dry dissection of pellets. Pellets must not be left in the NaOH solution more than 4 hours because teeth may become dislodged, reducing the chance of specific identification of mammalian prey remains. Chitinous materials also are unaffected by NaOH and are easily recovered, but any hair or feathers will be dissolved. Thus, this technique should not be used if the intent is to identify prey by the use of hair or feathers.

Skulls and dentaries are the most useful remains for identifying and counting mammalian prey, and a hand lens or low-power dissecting scope will be necessary in many cases to examine these prey remains. Limb bones and pelvic girdles also are helpful, especially for counting larger prey. Keys may aid in identifying small mammals (Stains 1959, Glass 1973, DeBlase and Martin 1974). Reference collections and investigator experience, though, usually are better than keys because skulls in pellets often are broken and may be missing diagnostic parts needed by keys. Thus, side-by-side comparison with skulls from reference collections is preferred. Mammalian hair from pellets also may be used to identify prey from raptors that digest bone or do not swallow it. Hair has little value however, for quantifying the prey consumed. Adorjan and Kolenosky (1969) and Moore et al. (1974) developed keys for identifying mammalian hair, and Korschgen (1980) gives instructions for preparing reference slides for hair. Feathers in pellets create similar but even greater problems than hairs. Feathers recovered from pellets typically require cleaning before they can be identified. Sabo and Laybourne (1994) provide techniques for feather preparation and also clues useful in identifying individual feathers.

Small mammals usually are enumerated in pellet samples by counting skulls and considering dentaries

and leg bones as a backup, especially if decapitation of prey is suspected. For larger mammal species, fragments should be assembled from a sample (skulls, dentaries, pelvic bones, and heads of limb bones) and then pieced together to estimate how many individuals were consumed (see Mollhagen et al. [1972] for more details). This procedure assumes that all parts of the prey were eaten and that all pellets containing the remains were recovered. Thus, counts based on this method most likely will be conservative. If possible, an additional technique should be used as a check.

Identifying bird prey is possible from feathers, beaks, and feet but often is difficult to accomplish without a large reference collection. Skulls, sterna, and synsacra are most useful for counting birds in pellets. Experts with access to extensive reference collections may be able to identify bone fragments and individual feathers to genus or species.

Bones of amphibians and bones and scales of fish and reptiles should be retained for identification. Collections of fish opercula at and around nests have been used to identify the prey of Osprey (Newsome 1977, Prevost 1977, Van Daele and Van Daele 1982). Comparison with reference material and consultation with experts on these taxa are recommended for identification.

Insects and other invertebrate prey also pose problems. The exoskeleton of arthropods is the only portion not digested by raptors, but often it is highly fragmented, making keys of little value as identification aids. Again, a good reference collection and consultation with experts are the best approaches to identifying those remains.

Pellet analysis offers advantages over other techniques—a large sample often may be acquired with relatively little expense, time, or disturbance of the raptors, and both seasonal and yearly trends in diet can be obtained, often from the same birds. Disadvantages are that pellets of some raptors, particularly falconiforms, do not always contain remains of a significant portion of prey eaten. For this reason, less confidence is possible from analysis of most falconiform pellets and from pellets of large owls preying on large prey. Available evidence indicates that pellet analysis is an excellent technique for medium-sized and smaller owls, e.g., Boreal Owl (*Aegolius funereus*) (Korpimäki 1988) and Eurasian Pygmy Owl (*Glaucidium passerinum*) (Kellomäki 1977), but slightly less reliable for insectivorous owls, e.g., Burrowing Owl (*Athene cunicularia*) and Flammulated Owl (*Otus flammeolus*), because their prey remains may be very small and pellets consisting of insect parts decompose rapidly (Marti 1974). Pellet analysis also appears to be a good method to study diet variation of Common Kestrels (*Falco tinnunculus*) using small rodents as their main foods, but also including many insects as alternative prey (Korpimäki 1985, Itämies and Korpimäki 1987). Although some investigations of falconiform diets have used pellet analysis exclusively (see references in Sherrod 1978), we recommend that a second method be used to check the accuracy of data from pellet analysis. On the other hand, Ritchie (1982) recommended using pellet analysis to complement studies based primarily upon prey remains in nests.

Contents of the Digestive System

Most early studies of raptor food habits were based upon examination of prey remains in raptor stomachs (Fisher 1893, McAtee 1935). This technique has no place in modern research or management practice except where a source of dead raptors, such as road kills, is available. Killing enough raptors to obtain a sample size sufficient to characterize diet is highly undesirable because the populations of most raptors are relatively small. The quantity of data obtained from an individual raptor using this technique is minimal compared with all the other available methods. The procedure for stomach analysis is simply to open the stomachs and crops of dead raptors and examine the contents. Identification and quantification of prey are similar to the processes described under pellet analysis. If analysis cannot be done immediately, stomachs can be frozen or preserved in 10% formalin until examined (Korschgen 1980).

If it is essential to examine stomach contents of live raptors, an emetic technique should be considered (Tomback 1975). Pulin and Lefebvre (1995) employed an antimony potassium tartrate (tartar emetic) on 137 bird species from 29 families. This technique apparently has not been tried on raptors and its safety is not known. Rosenberg and Cooper (1990) recommended flushing the digestive tract or forcing regurgitation with warm water instead of an emetic.

Another alternative for studying freshly eaten food without killing raptors is to massage food out of the crops of nestling or captured falconiforms (owls do not have crops) (Errington 1932). Workers with little experience in handling young raptors should avoid this practice because of the possibility of damaging the esophagus (Sherrod 1978).

Uneaten Prey Remains

Examination of nests for uneaten prey has proved useful by itself or in conjunction with other techniques (Craighead and Craighead 1956, Smith and Murphy 1973, Collopy 1983a). In one study, Bureau of Land Management (BLM) crews (USDI 1979) entered nests of several falconiform species every 4 to 6 days to collect all inedible prey remains and pellets. Fresh prey was marked by collecting the head, feet, and tail, and the remainder was left in the nest. Each collection was then examined for diagnostic remains to ascertain the species and number of prey represented. Collopy (1983a) collected similar materials from Golden Eagle (*Aquila chrysaetos*) nests. He found that these samples were not significantly different in species composition from what he saw in direct observation of the nests, but that they did seriously underestimate biomass of prey eaten compared with direct observation. Rutz (2003) radio-tracked male Northern Goshawks (*Accipiter gentilis*) in order to locate all kills the birds made. He showed that the remains of some prey species are harder to find by visual scanning and may result in biased dietary determination.

Several important considerations must be noted when collecting and interpreting prey remains in raptor nests. Larger, heavier bones may persist longer in the nest and cause overestimation of larger prey types. K. Steenhof (pers. comm.) suggests that collection intervals of 5 days or less help reduce this problem. Bones of smaller prey may be consumed at a higher rate (Mollhagen et al. 1972) or lost in the nest structure, causing underestimation of their contribution to a diet. Snyder and Wiley (1976) found similar circumstances at Red-shouldered Hawk (*Buteo lineatus*) nests. According to Bielefeldt et al. (1992), indirect collection of Cooper's Hawk (*A. cooperii*) prey remains near nests (92% birds) overestimated the proportion of avian items in comparison with direct observation of prey deliveries to nestlings (51–68% birds); most avian items brought to nestlings in their Wisconsin study, as elsewhere, were young birds. Thus, they suggest that other studies relying on indirect methods and using prey species' adult mass to calculate avian biomass probably have been biased toward birds among prey remains.

One potentially serious problem associated with collecting prey remains from nests is disturbance of the raptors. Caution must be taken to avoid keeping adults away from nests when weather conditions are detrimental to the young and to avoid any other excessive interference with normal behavior at the nest (Chapter 19). Another danger is that repeated visits may increase the likelihood of leading predators to the nests of some raptors.

Prey remains also may be recovered at plucking posts for some species, especially falcons, accipiters, and owls in the genus *Glaucidium*. Special care should be taken in interpreting such materials, particularly when using this method in conjunction with pellet analysis. Reynolds and Meslow (1984) collected pellets and other prey remains every 3 to 6 days at Cooper's Hawk nests and associated plucking sites, and Boal and Mannan (1994) used the same method in studying Northern Goshawks. They attempted to reconstruct and count each kind of prey by matching rectrices, remiges, and bills of birds, and fur, skull fragments, and feet of mammals from all material collected at each visit. Ziesemer (1981) discovered a bias in numbers of different prey types recovered by searching for plucking posts — birds were more readily found because of scattered feathers and prey larger than a single meal were often missed because of scavenging by mammals.

Some raptors store excess prey, which also can be a source of food habits information. Korpimäki (1987a) found that Boreal Owls stored prey mainly during the breeding season in the nest cavity, but Eurasian Pygmy Owls store prey mainly in the winter (Solheim 1984). Food storing also has been documented in the Northern Hawk-Owl (*Surnia ulula*) (Ritchie 1980), and Barn Owl (Marti et al. 2005), Eleonora's Falcon (*F. eleonora*) (Vaughan 1961), Merlin (*F. columbarius*) (Pitcher et al. 1979), and American Kestrel (Collopy 1977).

Direct Observation

Direct visual observations, while requiring a great deal of investigator time, offer some advantages over other techniques. This method is used most often at nests with the observer concealed in a nearby blind (Collopy 1983a, Sitter 1983, Younk and Bechard 1994, Rosenfield et al. 1995, Real 1996, Dykstra et al. 2003, Meyer et al. 2004). Others have used direct observation of foraging raptors, often from a vehicle and with the aid of a spotting scope (Wakeley 1978, Bunn et al. 1982, Beissinger 1983, Collopy 1983b). The most satisfactory approach is to observe continually all day or night. This approach will usually include a significant amount of time when no prey deliveries are made. If shorter periods of observation are used, they should be rotated randomly to include all hours when the species is active.

Several investigators preferred direct observation to other methods (Snyder and Wiley 1976, Collopy 1983a,

Sitter 1983) and it may be the best technique to use for species whose pellets do not provide accurate representation of their diet. Southern (1969) discovered by observing Tawny Owls (*Strix aluco*) that they were feeding earthworms to their young, a fact that had not been apparent from pellet analysis. Collopy (1983a) found that observation provided the best means of estimating biomass of prey consumed; both the number and size of prey can be accurately determined.

Direct observation from blinds can provide some of the most complete and accurate information on the diets of many raptors, as well as useful data on behavior. The chief drawback is the great amount of observer time required, often under uncomfortable conditions, to obtain an adequate sample. Blinds should be constructed in short periods over several days to reduce disturbances. The best time to build blinds is before a traditionally used site is occupied, keeping in mind that the birds may not select that site in a particular year. Some species and even some individuals are sensitive to disturbance and may not tolerate blinds placed near the nest, whereas others will accept blinds as close as 2 m (Geer and Perrins 1981). Size of prey involved is another consideration in distance from blind to nest; insectivorous species will necessitate close placement of blinds in order to identify prey, but the prey of eagles can be identified up to 40 m away (Collopy 1983a). R. Reynolds (pers. comm.) cautions that estimating the size of small vertebrate prey by observation is difficult. Sitter (1983) preferred to observe Prairie Falcons (*F. mexicanus*) from about 15 m distant and slightly above the nest. R. Glinski (pers. comm.) placed blinds slightly below the nest to reduce disturbance. Regardless of the distance between blind and nest, binoculars or spotting scopes are usually needed to identify prey.

Cavity-nesting species also can be observed directly, but some modification of the site may be necessary and this technique should be used only with great caution. Southern (1969) used nest boxes with a partially cut-away side so that prey delivered to the young could be seen. Smith et al. (1972) installed a one-way mirror in an American Kestrel nest cavity, and one of us did the same in a Barn Owl nest box with blind attached (Marti 1989).

Nocturnal species, obviously, are harder to observe. Night-vision scopes or goggles (image intensifiers) provide the most satisfactory answer to this problem but are expensive; DeLong (1982) used one with good results at nests of Long-eared Owls. A simpler and less costly approach is to illuminate the nest with artificial light. Southern (1969) found that a red light placed at Tawny Owl nests did not disturb the birds, and a six-volt, clear flashlight bulb produced no behavioral changes in Barn Owls when placed just outside nest cavities or even within a nest box (Marti 1989). At distances of 10 to 60 m, aided with 7 x 50 binoculars, adult prey deliveries to nestlings could be monitored but the prey could not be identified. Prey was easily identified however, when deliveries were observed through a one-way mirror in the back of a Barn Owl nest box illuminated as described above.

Non-breeding raptors are harder to observe for documenting prey captured because of their mobility and, in many species, secretive habits. Roth and Lima (2003), employing radio-tracking to follow Cooper's Hawks in winter, were able to observe 179 attacks — 35 of which were successful — and identify the prey captured.

Confining Nestlings

Additional food-habits information has been acquired for 4 to 10 weeks beyond normal fledging times by tethering young raptors on the ground near their nests so that prey brought by the adults could be studied more easily (Errington 1932); tethers were similar to falconry jesses. Losses of young raptors to predators while using this method (as high as 50%) prompted Petersen and Keir (1976) to tether young on platforms off the ground. Care should be taken to adjust the length of the tether so that the young cannot hang over the edge of the platform. Selleck and Glading (1943) placed cages over young raptors in their nests. This forced adults to leave prey outside so it could be identified and counted. These workers found that the cage-nest technique worked well for Barn Owls but not as well for Northern Harriers, because of behavioral differences in prey delivery between the two species. Sulkava (1964) used this technique with success on Northern Goshawks in Finland.

These methods may be useful in studies of raptor species for which food-habits data are otherwise difficult to obtain, but they should be used sparingly and with great care. Increased predation upon the young, abandonment by the adults, and interference with normal behavioral development are inherent dangers.

Photographic and Digital Image Recording

Several generations of systems, from film to digital, have been described for monitoring wildlife activity including the use of cameras automatically triggered by

photocells (Dodge and Snyder 1960, Osterberg 1962, Cowardin and Ashe 1965, Browder et al. 1995, Danielson et al. 1996), cameras triggered by observers in blinds (Wille and Kam 1983), and automatic sampling using time-lapse cameras or video recorders (see references below).

Single-lens, reflex, 35-mm cameras, the first camera type employed for raptor food-habits monitoring, have many accessories helpful in remote or automatic operation (e.g., auto-winders, telephoto and close-up lenses, bulk-film backs, and radio-controlled shutter releases), or both. Users have reported that the 35-mm format provides good resolution for identifying prey, but the cost of equipment, film, and film processing is high. Another drawback of this technique, one shared with other similar techniques, is that many photographs are under- or over-exposed and others do not show prey clearly enough to allow identification.

Another monitoring option is to sample automatically by using a time-lapse camera set to take one or more frames at constant intervals throughout the sampling period. Time-lapse photography has been used to study raptor diets since the early 1970s when Temple (1972) described one of the first portable systems using a super-eight camera that could be installed at raptor nests and programmed to expose images at set time intervals, usually one frame every 1 to 5 minutes. Similar systems were used to study a variety of nesting raptor species (Enderson et al. 1972, Franklin 1988, Tømmeraas 1989, Hunt et al. 1992). However, super-eight cameras are no longer easily available and film is difficult to find and have processed.

A number of video-camera systems can be used for recording the diets of diurnal raptors (Kristan et al. 1996, Delaney et al. 1998, Booms and Fuller 2003a). Lewis et al. (2004a) designed a video-surveillance system to document the diet of Northern Goshawks consisting of a miniature video camera, time-lapse video recorder, and a portable 13-cm television, powered with a single, deep-cycle marine battery.

Recent advances in time-lapse video surveillance systems have made videography a far more useful technique for recording diets of raptors. If the species of interest is sensitive to disturbance, cameras can be placed so that recording equipment and power sources are well away from its nest and visits to replace batteries and tapes can be made daily or at intervals of two to three days. Time-lapse videography is versatile and accommodates options for capturing images from real-time (20 frames/second) to 960-hour time-lapse (0.25 frames/second) on a standard 8-hour VHS videotape. To maximize the number of frames of each prey delivery while maximizing the interval between visits to change videotapes, the systems can be programmed to record at various frames/second and at specified times of the day.

Solar-powered surveillance systems are useful if routine replacement of batteries is difficult. Booms and Fuller (2003a) used solar-powered, time-lapse Sentinel All-Weather Video Surveillance Systems (Sandpiper Technologies Inc., Manteca, California) to record prey deliveries to Gyrfalcon (*F. rusticolus*) nests in Greenland. Video cameras were mounted within 1 m of nests and all other equipment was installed at the bases of nest cliffs where a time-lapse VCR was used to record images from the camera. The recording unit was placed in a location that allowed easy and safe access to change tapes while not being detected by the adult birds. Cameras were installed during mid- to late incubation, and nests were not visited again until after young had fledged.

Solar-powered, radio-frequency linked, transmitting video camera systems also are available for use with species that are sensitive to repeated disturbances near their nesting areas. These systems transmit video signals from the nest site to a remote receiver and disturbance at nest sites is minimal because personnel do not need to visit nesting areas to change videotapes or batteries. Kristan et al. (1996) used such a system that performed reliably up to 8 km, to document prey delivered to Osprey nests in California. While the cost of the system was approximately $6,100 (U.S.), the savings in personnel time were substantial.

Video systems using miniature, infrared-sensitive video cameras equipped with infrared light-emitting diodes and time-lapse video recorders have proved to be effective in documenting the dietary habits of several species of owls. Proudfoot and Beasom (1997) used such a camera and light source to record prey deliveries to nests of Ferruginous Pygmy-Owls (*G. brasilianum*) and Delaney et al. (1998) used a similar system to study Mexican Spotted Owls (*S. occidentalis*). A useful range up to 3 m in total darkness was possible with the aid of six infrared light-emitting diodes. Video images were recorded using time-lapse VHS recorders connected to cameras via coaxial cables. Each tape provided 24-hour coverage when recording at approximately five frames/second. These camera systems were powered by either 12-volt, deep-cycle marine batteries or 12-volt, sealed-gel-cell batteries. The latter are rugged and reduce the potential for spillage during

backpack transport. Oleyar et al. (2003) described an inexpensive camera system designed to study the diet of Flammulated Owls. This system used a miniature pinhole, infrared camera and a single infrared-emitting diode connected to an 8-mm camcorder to record prey deliveries on tape. The camera system was powered by three batteries: a 6-volt camcorder battery, a 1.5-volt battery for the infrared diode, and a 9-volt battery for the camera. Cameras were turned on each night and allowed to record until the batteries failed, which was generally at about two hours.

Images recorded on videotapes can be viewed using VCR equipment and a color TV monitor. Many VCRs allow frames to be replayed at different speeds and each frame can be frozen for inspection.

Comparing Collection Methodologies

It is obvious from the information presented above that different raptor species require different methods for collecting unbiased food-habits material. A number of investigators have used multiple methods on the same species and offer insights on which method is best, and when it may be appropriate to use more than one method of collection. Pavez et al. (1992), Real (1996), and Sequin et al. (1998) made direct observations at nests of Black-chested Buzzard-Eagles (*Geranoaetus melanoleucus*), Bonelli's Eagles (*Hieraaetus fasciatus*), and Golden Eagles, respectively, and compared prey counted by observation with prey identified in pellets and uneaten remains in the nest. For Black-chested Buzzard-Eagles, pellet contents under-represented birds whereas insects were over-represented by observation and under-represented by prey remains. In the case of Bonelli's Eagle, prey remains were collected under two regimens—fresh remains while nestlings were in the nest and old remains collected after breeding finished. Pellets also were collected; using old prey remains was the only method that differed significantly from observations and Real (1996) concluded that pellet analysis was the most efficient method for studying Bonelli's Eagle diet. Sequin et al. (1998) recommended that combining pellet contents and prey remains is the best procedure if direct observations cannot be made. Mersmann et al. (1992) compared three techniques for studying Bald Eagles (*Haliaeetus leucocephalus*). Direct observations resulted in biases toward easily identified species such as eels, but also permitted documenting consumption of small soft-bodied fish that were not well detected by other methods. Using captive eagles, Mersmann et al. (1992) discovered that fish were under-represented in the pellets, but that most birds and mammals eaten were detected. Analysis of food remains of the captive eagles over-represented birds, medium-sized mammals, and large, bony fish; small mammals and small fish were under-represented.

Sharp et al. (2002) and Marchesi et al. (2002) compared diets obtained through pellet analysis and uneaten prey remains for Wedge-tailed Eagles (*Aquila audax*) and Eurasian Eagle-Owls (*Bubo bubo*), respectively. Sharp et al. (2002) concluded that combining data from the two methods may result in a biased diet determination and recommended that results for the two techniques be reported separately. On the other hand, Marchesi et al. (2002) recommended combining data from the two techniques, but indicating the relative contribution of each method in the pooled sample; they found that prey remains over-represented birds and large prey in general, under-represented mammals, and failed to detect fish. Pellets gave a more realistic picture of diet but failed to detect many birds identified in prey remains.

Studying Barn Owl diets, Taylor (1994) compared prey delivered to nests as recorded by continual photographic monitoring with contents of pellets produced during the same period; results of the two techniques agreed closely. Comparison of prey remain collections, pellet contents, and prey delivery videography showed that videography provided the most complete descriptions and least biased data on the diets of Northern Goshawks and Gyrfalcons (Booms and Fuller 2003b, Lewis et al. 2004b). Additionally, Lewis et al. (2004b) felt that videography equipment and its maintenance is cost-effective compared to human-resource costs associated with prolonged direct observations made from blinds.

INTERPRETATION OF RAPTOR DIETS

Quantification

Raptor diets can be quantified in a number of ways depending upon the needs and objectives of the analysis. One common method is to calculate the percentage of occurrence by number for each prey category in the total sample. In cases where it is not possible to count the number of each prey, diets may be quantified by giving the percentage of samples (e.g., pellets or nest contents) in which each kind of prey occurred. Diets also

can be quantified by the relative contribution of the various prey types to the total weight (biomass) of prey consumed. Both frequency and biomass methods have value. For example, frequency data provide useful information on the relative impact a raptor has upon various prey species, whereas biomass determination may give a more accurate evaluation of the relative importance of prey species to the diet of a raptor (i.e., one rabbit provides the equivalent energy of many mice).

Frequency by number of prey (species or other taxon) is calculated by dividing the number of individuals in each identifiable category of prey by the total number of prey in the sample. When prey are identified by hair or feather analysis, obviously it is not possible to count the number of individuals in a sample. In these and other cases where it is not possible to count numbers of individual prey, frequency of occurrence may be used. This may be calculated, for example, by dividing the total number of pellets in a sample into the number of pellets in which each kind of prey was found; the disadvantage of analyzing dietary data using this approach is that these data cannot be used to calculate niche metrics, which are described below.

Biomass of prey in a diet sample usually is estimated by multiplying the number of individuals of each prey species by the mean weight of that prey. Biomass is then expressed as the proportion each prey species (or other taxa) contributed to the total weight consumed. Several sources provide tables of weights for this purpose (Smith and Murphy 1973, Marti 1974, Brough 1983, Steenhof 1983, Dunning 1984), but locally obtained prey specimens, when available, may provide more accurate weight information. In many cases prey should be assigned to different weight categories according to age and sex for more accurate estimates of dietary biomass. If raptors select other than average-sized prey of a particular species, biomass estimates derived in the above manner will be biased (Santibáñez and Jaksic 1999). Sometimes greater accuracy may be obtained by measuring or estimating weights of prey actually eaten, as determined through direct observation, examination of whole prey in nests, or photographic techniques. Prey weights also can be estimated from measurements of skeletal remains in uneaten prey remains (Diller and Johnson 1982, Woffinden and Murphy 1982) and pellets (Boonstra 1977, Goszczynski 1977, Morris 1979, Nilsson 1984). Fairley and Smal (1988) provide correction factors for more accurate estimation of the mass of prey eaten from measurements of bones found in pellets. Norrdahl and Korpimäki (2002) warned that body mass of some small mammals can vary considerably among years, especially in species that undergo cyclic population fluctuations. If this is occurring, it must be accounted for in estimating biomass of prey consumed by raptors.

Wijnandts (1984) obtained weights of prey delivered to nestlings by placing nests containing nestling Long-eared Owls on platforms equipped with electronic balances. He reported that accuracy depended upon wind speed and stability of the supporting tree but was usually within ± 2 g. This technique would seem to be applicable to many raptor species.

Diversity

Diversity is an expression of community structure wherein groups of organisms (identified to species or higher taxa) are characterized by the number of categories in the group and the relative number of individuals in each category (Magurran 1988). Measures of diversity are employed to examine the structure of assemblages such as the prey species in a raptor's diet. Properly used, diversity indexes allow the summarization of large quantities of data as a single value. These indexes have been used as a quantitative measure of niche breadth (Pielou 1972, Hurtubia 1973) and, as such, to characterize and compare raptor diets (Jaksic et al. 1982, Marks and Marti 1984, Steenhof and Kochert 1985, Bellocq 2000). Korpimäki (1987b, 1992) related the variation in diet diversity to variation in breeding density and reproductive success.

Below we use the terms diversity and food-niche breadth synonymously. Diversity has two components, richness (the number of prey categories, species or other) and evenness (how uniformly represented the various kinds of prey are) (Margalef 1958, Pielou 1966). A raptor's diet has high diversity (i.e., represents a broader food niche) if many species are included in nearly equal numbers. Conversely, a collection consisting of few species or with species represented in very different abundances has low diversity (represents a more narrow food niche).

Several assumptions, some stringent, must be met in collecting data for calculating diversity indexes. See discussions of these in Pielou (1969), Brower and Zar (1984), and Hair (1980). Much has been published on the relative value of different diversity indexes, including opinions by some authors that these indexes have no value (Hurlbert 1971). Others, though, found them very

useful (Hill 1973). A comprehensive coverage of the problems in measuring diversity is not appropriate here, but see Greene and Jaksic (1983), Kinako (1983) and Ghent (1991) for background, criticisms, and precautions in using these indexes.

Greene and Jaksic (1983) present information directly useful for the interpretation of diversity indexes. Not surprisingly, they found that high resolution of categories (identification of prey to species or genus) compared to low resolution (identification of prey to order or class) yields greater niche breadths, and that high resolution more consistently measures the extent to which raptors affect various prey populations. Low resolution of prey, though, may be useful in comparing functional niches; broader niches at this level, in comparisons among raptor species, may indicate a more versatile predator (e.g., a predator able to consume prey presenting many different kinds of problems in capture and handling).

Many measures of diversity have been devised and are in current use (Washington 1984). See Brower and Zar (1984), Hair (1980), and Ghent (1991) present and compare many of the commonly used indexes. Only a few of the most widely employed indexes are covered here (examples of the calculation of these and the following evenness indexes are in Appendix 1).

Simpson (1949) was the first to devise an index incorporating both richness and evenness:

$$D = \Sigma\, p_i^2,$$

where p_i is the relative proportion of each member of the assemblage being investigated. This index yields values from zero to one. When calculated with this formula, Simpson's index actually measures dominance (i.e., larger values indicate lower diversity in the assemblage) (Whittaker 1965). For example, a raptor diet heavily dominated by one or two kinds of prey will yield values close to one in the Simpson's index, whereas a diet containing a more even distribution of prey types (higher diversity) will yield a value closer to zero. In order to convert Simpson's index to a more interpretable measure of diversity (i.e., where larger values of the index reflect greater diversity), it is common to calculate $1/D$ (Levins 1968) or $1\text{-}D$ (Odum 1983). Ghent (1991) recommended using Simpson's index because it is the simplest diversity index that adequately performs its task.

Shannon's index (Shannon and Weaver 1949) is another measure of diversity widely used in ecology. The formula is:

$$H' = -\Sigma\, p_i \log p_i,$$

where p_i represents the proportion of each species in the sample. The larger the value obtained for H' (or antilog H'), the greater the diversity of the sample. Any logarithmic base can be used as long as consistency is maintained throughout. However, indexes calculated with different logarithmic bases must be converted to the same base before comparisons between them are meaningful. Brower and Zar (1984) list appropriate conversion factors. The antilog of H' is more readily interpretable as a measure of diversity than H' because it is linearly related to the number of prey categories in the sample (Hill 1973, Alatalo and Alatalo 1977).

Even though both Simpson's and Shannon's indexes measure richness and evenness, DeJong (1975) found that Shannon's index places nearly twice as much weight on the richness component than does Simpson's. Conversely, Simpson's is influenced by evenness much more than Shannon's.

Colwell and Futuyma (1971) developed a standardized measure of food-niche breadth (FNB) that permits meaningful comparisons between diets of different species or the same species in different geographic areas:

$$FNB_{sta} = (B_{obs} - B_{min}) / (B_{max} - B_{min}),$$

where B_{obs} is the reciprocal of Simpson's Index, B_{min} is the minimum niche breadth possible (equals one), and B_{max} is the maximum breadth possible ($= N$). See Jaksic and Braker (1983) and Marti (1988) for examples of its use in comparing food-niche breadth among geographical areas where differing numbers of prey were available to widespread raptors.

No easy way exists to determine what constitutes an adequate sample size for calculating dietary diversity. Larger samples are more likely to include rare prey, thus increasing the measure of diversity (although the lack of including rare prey has little effect on Shannon's index [Brower and Zar 1984]). Many factors, though, complicate the situation: density, number of species, and availability of prey. For example, a large diet sample that yields a narrow estimate of food-niche breadth might indicate that only a small number of prey species was available to the predator. Conversely, it might indicate that a larger assemblage of available prey species con-

tained one or a few prey that were particularly abundant or vulnerable to the predator. Competition, either by exploitation or interference, also could affect how a predator exploits prey species and thus alter its dietary diversity. Extensive literature exists on the influence of competition upon food-niche breadth, but coverage of it is beyond the scope of this chapter.

One means of determining the sample size needed to accurately reflect the number of prey types in a raptor's diet is to plot the number of new prey species occurring per sample as a function of sample size; when an asymptote is reached, a sufficient sample size has been obtained (Heck et al. 1975, Gotelli and Colwell 2001). As sample size increases, more species will be recorded with the sampling curve rising rapidly at first and then more slowly as increasingly rare species are included. See Green and Young (1993) for formulas to estimate the sample size needed to detect rare species.

We provide several populations (Appendix 2) to illustrate the required sample size on estimating species richness and diet diversity of the populations from which samples are drawn. Two of these are simulated populations; the other is a sample of actual dietary data from a population of Barn Owls. From each population, we drew random samples with replacement ranging from 5 to 500 individuals in increments of five. Each sample size was repeated 100 times after which the mean number of prey types (richness) and mean sample diversity (reciprocal of Simpson's index) were calculated. The results in Fig. 1 illustrate that when species richness is very low (five, population A, Appendix 2), a sample of less than 20 individuals will include all potential species. When species richness doubles to 10 (population B, Appendix 2), a sample of about 50 individuals is required to include all potential species (Fig. 2). The simulated populations A and B have maximum evenness (i.e., all prey species are present in exactly the same numbers). In contrast, population C (Appendix 2) has 29 prey species but is dominated by two species and only six species are common; a sample size of less than 20 will include six species, but many prey species are rare and a sample size of 1,000 only includes about 50% of the potential prey types.

When trying to estimate diversity, the situation is reversed. The two populations with maximum evenness (A and B) require sample sizes of more than 100 to approach an asymptote. The yield of additional information when sample sizes are more than 100 is slight, and samples of even 500 individuals do not quite reach an estimation of the population's true diversity (Figs. 1

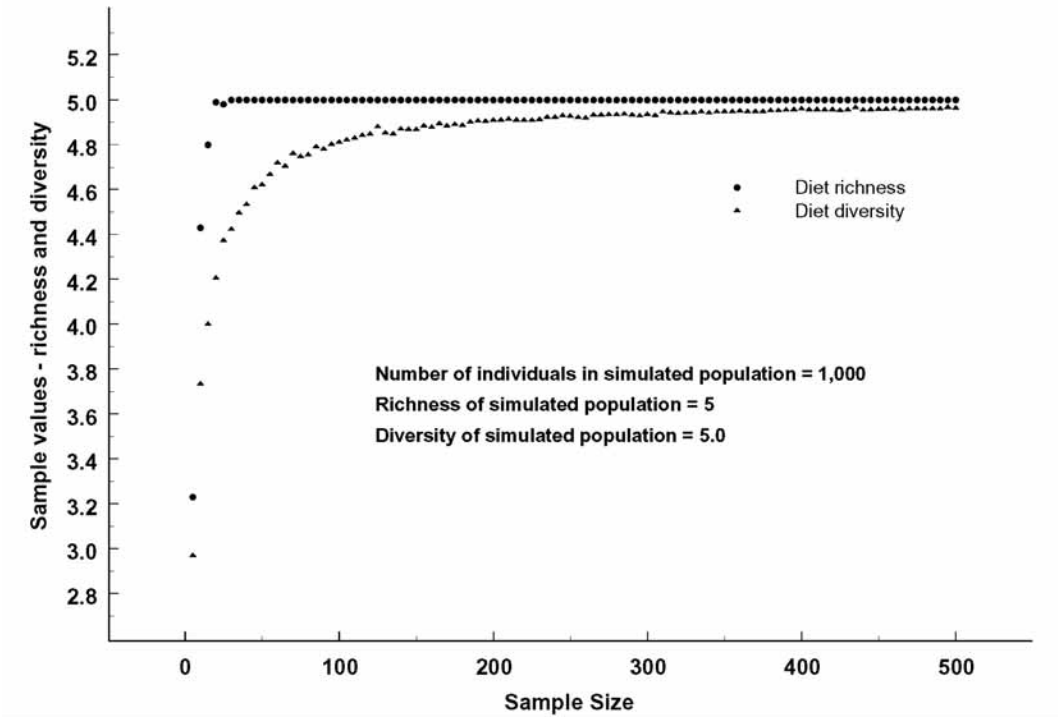

Figure 1. Diet richness and diversity of samples drawn from a simulated population with low richness and high evenness to illustrate the sample size needed to adequately characterize that of the sampled population.

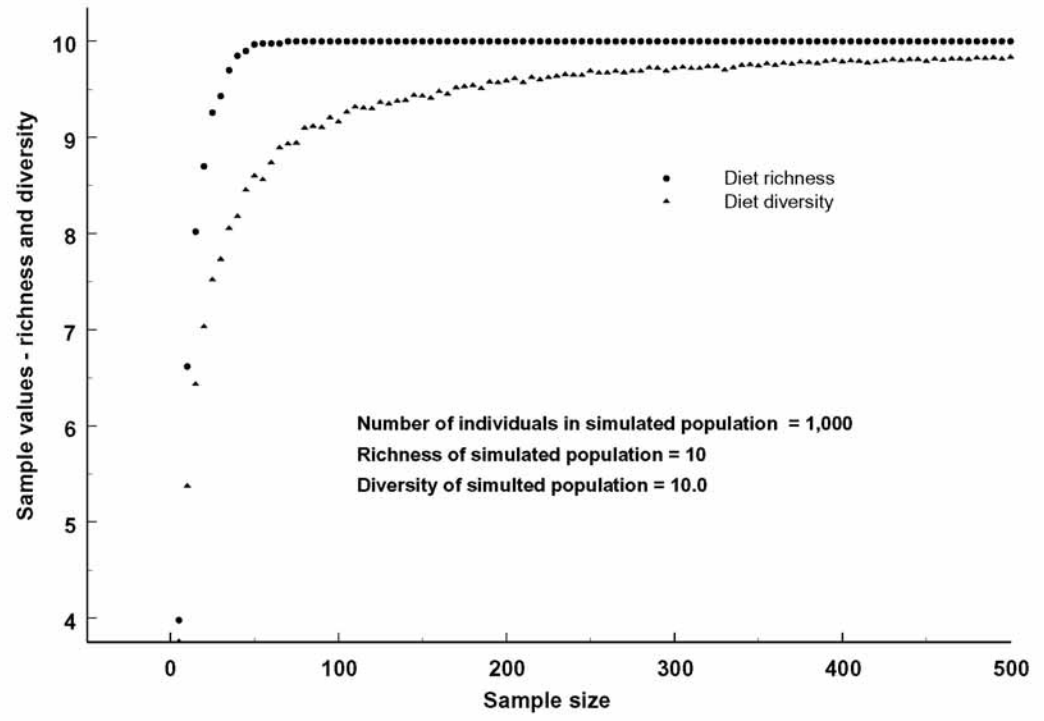

Figure 2. Diet richness and diversity of samples drawn from a simulated population with higher richness and high evenness to illustrate the sample size needed to adequately characterize that of the sampled population.

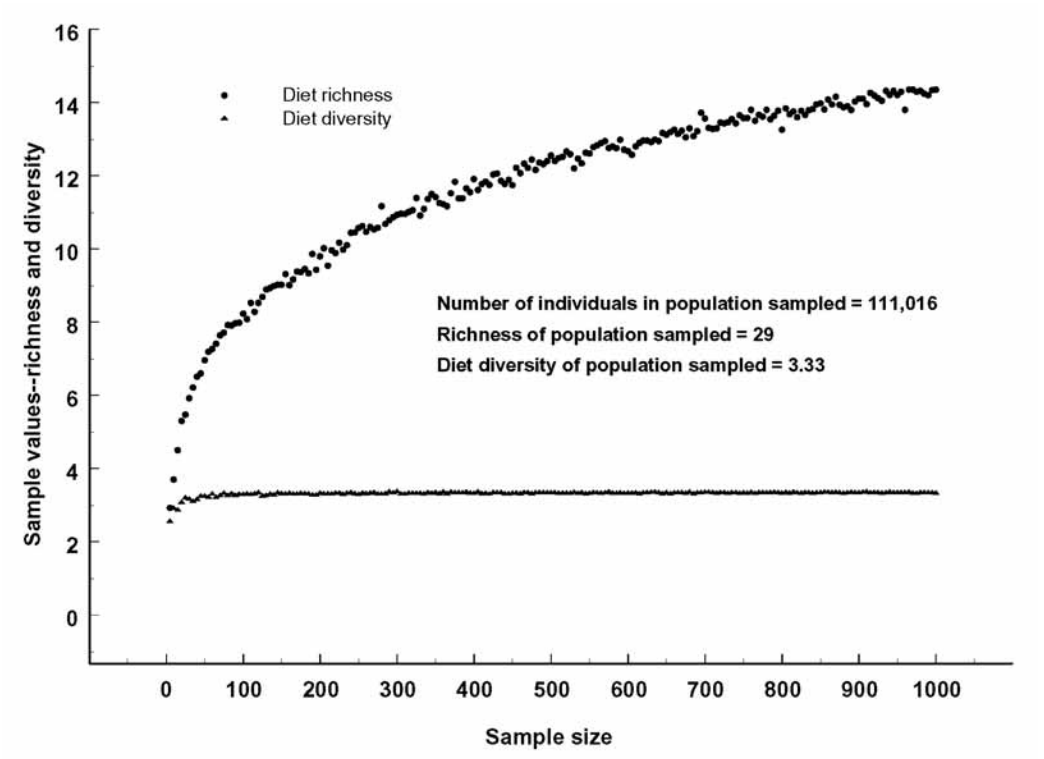

Figure 3. Diet richness and diversity of samples drawn from an actual population with high richness and low evenness to illustrate the sample size needed to adequately characterize that of the sampled population.

and 2). In contrast, population C needs samples of only 50 to 100 individuals to correctly estimate the diversity of the population and larger samples offer no additional information about diversity (Fig. 3).

Often, biologists are interested in identifying the common or dominant prey in a raptor's diet (i.e., those that make significant contributions of energy). Prey species taken rarely are of incidental interest. They show the widest range of the raptor's diet, but contribute little to the energy intake. In such situations, we suggest that samples of around 100 prey individuals are sufficient to give a reasonable approximation of a raptor's diet. This is not to say that samples that small are always ample. If the goal is to understand variation (e.g., geographic or temporal), many samples of 100 or more from different individual raptors or from different times (seasons, years) will be needed.

As noted, diversity indexes include both the richness and evenness of a sample, but it is often desirable to provide separate measures of the two components. Richness is simply expressed as the number of species (or other taxa) in a raptor's diet, and several approaches to measuring evenness or equitability have been developed (Pielou 1969, Hurlbert 1971, Hill 1973). Frequently used is Pielou's (1969):

$$J' = H' / H\,max',$$

where H' is the diversity value calculated from Shannon's index, and $H\,max'$ is the logarithm of the number of species (species richness) employing the same logarithmic base used in the calculation of H'. Because species richness (i.e., the number of prey actually eaten by the raptor) is often underestimated in a dietary sample, J' tends to overestimate evenness. Alatalo (1981) modified Hill's (1973) ratio to develop a more interpretable measure of evenness:

$$F = (N_2 - 1) / (N_1 - 1),$$

where N_1 is the antilog of Shannon's index (H') and N_2 is the reciprocal of Simpson's index ($1/D$). Alatalo (1981) cautioned that there is no single mathematical definition of evenness; each measure weights different properties of abundance distributions in different ways.

Another technique for comparing dietary prey frequencies with relative availability of prey is Ivlev's (1961) selectivity index:

$$S = (r - p) / (r + p),$$

where r is the proportion of prey taken by the predator and p is the proportion of the same prey available to the raptor. This index ranges from –1 to + 1. Values near + 1, 0, and –1 indicate a prey type taken above, at, and below its availability, respectively. This method has been applied to an experimental study of prey selection in a raptor (Marti and Hogue 1979). Ivlev's approach is useful however, only to compare prey species one at a time and does not allow simultaneous comparison of the entire spectrum of prey in a diet with its availability.

The chief drawback to the indexes described above and many other diversity indexes is that they assume that all resources are equally available. Measures that consider resource availability have been developed and should be considered for use if adequate data on prey availability can be obtained (Petraitis 1979, 1981; Feinsinger et al. 1981, Bechard 1982). One problem remains even with these measures: does the raptor perceive relative availability of prey in the same way the investigator does? This is similar to a problem in the measurement of dietary diversity by any method: do the prey categories (species or other) chosen by the investigator correspond to real differences among prey as perceived by raptors? Prey choice has been studied by identifying prey captured by raptors and comparing it with estimates of the availability of prey in the vicinity by live- or snap-trapping small mammals, censusing birds, or both (Kellomäki 1977, Koivunen et al. 1996a, 1996b).

Index of Relative Importance

The index of relative importance (IRI) is another composite measure combining three means of characterizing a diet sample: (1) the number of prey in a sample, (2) the volume or mass of each kind of prey in a sample, (3) and the frequency of occurrence for a kind of prey in a sample (i.e., the percentage of pellets in a sample of pellets that contain the prey in question). Introduced in the fishery literature (Pinkas 1971, Pinkas et al. 1971), it rarely has been used for terrestrial predators, but Hart et al. (2002) recently promoted its use for a wider taxonomic array including birds. IRI is calculated as:

$$IRI = (N + V)F,$$

where N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage. Martin et al. (1996) substituted mass for volume in their

analysis of the diets of feral cats using this formula. Hart et al. (2002) applied the method to Barn Owls, the only application we know of for a raptor, but it may be a technique potentially valuable to raptor biologists.

Rarefaction

Rarefaction is a statistical method for estimating the number of species expected to be present in a random sample of individuals taken from any given collection and is a powerful standardization technique (Gotelli and Colwell 2001). Rarefaction is an appropriate tool for defining community structure and has been used in comparing species richness among communities in various ecosystems. Estimating community diversity by rarefaction provides an alternative that avoids some of the difficulties of calculating species richness by scaling down all collections to the same sample size (Hurlbert 1971, Heck et al. 1975).

Because a larger sample should contain more species, it may often be of interest to estimate how many species would be expected in smaller samples from the same population. From the number of individuals of each species in an original collection, a series can be calculated that reflects the numbers of species present in each smaller subset randomly drawn from the original collection. This method estimates not only species richness, but also the confidence limits for this parameter (Heck et al. 1975). Doing this allows you to compare statistically raptor diets with different species richness. The technique also allows for the generation of a rarefaction curve the shape of which is a graphic display of accumulation rates of relative abundance; therefore, the evenness of diets can be compared by examining the steepness of the curves and their intersection (James and Rathbun 1981). In general, the steeper the rarefaction curve is, the higher the evenness.

Studies of food-web structure, especially when attempting to determine the putative association between a factor such as productivity and a measure of food-web connectivity, depend heavily on using rarefaction procedures. For instance, Arim and Jaksic (2005) knew that the total number of prey identified affected the number of trophic links estimated per species and controlled for the effect of variation in sample size with a rarefaction procedure. Considering the types of prey present in raptor diets, several rarefaction procedures may be conducted (e.g., one for vertebrate and another for invertebrate prey), and the expected richness from both rarefactions can then be added. For more omnivorous raptors, even a third prey type might be used. A rarefaction calculator is available online: www2.biology.ualberta.ca/jbrzusto/rarefact.php (last accessed 11 January 2007).

Mean Prey Weight

Diets of predatory birds also can be quantified by estimating the mean mass for all prey in a diet sample. This grand mean is calculated by multiplying the total number of each kind of prey by the mean mass for that species, then summing these totals and dividing the sum by the total mass of prey individuals in the sample. Estimating the grand mean mass of prey is subject to several potential problems. Frequencies of prey masses in a sample of raptor food cannot be assumed to follow normal distributions because the masses of prey eaten often are skewed to one side of the mean. Also, mean mass of prey calculated in the manner described is sensitive to very large or very small prey, even if they occur in low frequencies. Problems caused by these conditions can by minimized by log-transformation of the mean masses of individual prey species prior to calculating the grand mean prey mass. The re-transformed mean (antilog) of the log-transformed masses is called the geometric mean (Sokal and Rohlf 1995).

Estimation of mean prey mass also is subject to the same problems and biases discussed in biomass quantification above. Despite this, this approach has been used successfully to characterize and compare the diets of many raptors (Storer 1966, Jaksic et al. 1981, Marks and Marti 1984, Steenhof and Kochert 1985).

Dietary Overlap

Another useful technique for making comparisons between two raptor diets is dietary overlap or similarity—the degree of joint use of prey species. Dietary overlap may be used in comparing diets of different species, comparing diets of the same species in different areas or times, and other similar comparisons. An objective measure of overlap is required to quantify such comparisons; many methods have been proposed (Levins 1968, Schoener 1968, Pianka 1973, Hurlbert 1978), but considerable disagreement still exists about which measure is superior (Ricklefs and Lau 1980, Slobodchikoff and Schulz 1980, Linton et al. 1981). The interpretation of overlap also lacks unanimity, especially in regard to its use as a measure of competition. Although niche overlap has been widely used as an

indicator of competition (MacArthur and Levins 1967, Cody 1974, May 1975), such use has been criticized (Colwell and Futuyma 1971, Pianka 1974, Abrams 1980). High overlap in the diets of two or more raptors could be an indication of competition or the result of abundant food resources being exploited by both species without competition (Lack 1946, Pianka 1974). Low overlap, on the other hand, has been viewed as an indicator of divergence caused by prior competitive interactions (Lawlor 1980). Changes in dietary overlap may reveal more about competition than the degree of overlap (Schoener 1982, Steenhof and Kochert 1985). Korpimäki (1987) found that when diets of Long-eared Owls and Common Kestrels overlapped, it decreased the reproductive success of both when they were breeding close together. Schoener (1982) in his review of dietary overlap studies concluded that changes in overlap often occurred between seasons and from year to year; most cases showed less overlap in lean times. Pianka's (1973) index has been widely used in comparing raptor diets (Jaksic et al. 1981, Steenhof and Kochert 1985, Marti et al. 1993a,b) and is calculated as:

$$O = \Sigma\, p_{ij}\, p_{ik} \sqrt{} \sqrt{} (\Sigma\, p_{ij}^2, \Sigma\, p_{ik}^2),$$

where p_{ij} and p_{ik} are proportions of prey species (or other prey taxa) in the diets of raptors j and k, respectively. Values obtained range from zero (indicating no overlap) to one (indicating complete overlap). An illustration of the calculation of this overlap index is included in Appendix 1.

Several investigators have devised methods of weighting availability or abundance for more accurate calculation of the joint use of resources by two species (Colwell and Futuyma 1971, Hanski 1978, Hurlbert 1978). Although few raptor studies will have data adequate to make use of these methods, investigators exploring resource overlap should be aware that they exist.

Community Trophic Ecology

The techniques discussed above can be useful in understanding how trophic factors contribute to the structure of ecological communities (Jaksic et al. 1981, Jaksic and Delibes 1987, Jaksic 1988, Bosakowski and Smith 1992, Marti et al. 1993a,b; Korpimäki and Marti 1995, Aumann 2001). Similarly, they may be used to compare the ecological roles of two species (Marks and Marti 1984, Donazar et al. 1989, Marti and Kochert 1995, Burton and Olsen 2000, Hamer et al. 2001). In addition, studies of food-web structure that attempt to disentangle the roles of predation and competition versus exogenous factors such as climate, still rely heavily on these apparently old-fashioned tools (Lima et al. 2002, Arim and Jaksic 2004).

Potential Use of Stable-Isotopes in Diet Analyses of Raptors

The analysis of trophic relationships in bird assemblages through conventional dietary assessments (e.g., stomach contents, prey remains, pellets, and feces) can be difficult, daunting, and biased because the determination of prey composition depends heavily on digestibility and on the nature of prey items (i.e., hard- versus soft-bodied). To resolve this bias, a complementary approach based on the use of stable isotopes has been gaining use. This approach relies on the ratios of stable isotopes of nitrogen (15N/14N, conventionally expressed as δ15N), and of carbon (13C/12C, or δ13C) in consumer proteins reflecting those of their prey in a predictable manner (DeNiro and Epstein 1978, 1981; Peterson and Fry 1987).

In the case of nitrogen, δ15N signature shows a stepwise enrichment at each successive level within a food chain (Hobson et al. 1994, Sydeman et al. 1997). As a result, predators occupying relatively high trophic positions have correspondingly elevated δ15N values. For carbon, δ13C values also may show a tendency to increase with trophic level, but to a lesser extent than that of δ15N (Hobson and Welch 1992). Nevertheless, the δ13C value can provide information about the source of carbon entering a food chain, for example, distinguishing between marine and freshwater systems (Mizutani et al. 1990) or discriminating between inshore versus benthic feeding and pelagic feeding in seabirds (Hobson et al. 1994).

In recent decades, the application of stable-isotopic analysis to studies of avian nutritional ecology and movement has increased tremendously. One of the important advances in this field has been the development of nondestructive sampling approaches that involve the isotopic analysis of bird feathers (Mizutani et al. 1990, Hobson and Clark 1992). Multiple stable-isotope analyses applied to investigations of entire seabird assemblages have yielded important insights into intra- and inter-specific trophic relationships, and have resolved trophic interactions on both spatial and temporal scales (Hobson et al. 1994). Dual-isotope mul-

tiple-source mixing models have been developed to quantify the proportions of various prey categories in the diet of carnivorous mammals (Ben-David et al. 1997), seabirds (Hobson 1995, Schmutz and Hobson 1998), and birds across a terrestrial-marine landscape (Harding and Stevens 2001), thus emphasizing the utility of stable isotopes in studies of diet and community trophic structure. To date, no such analyses have been attempted with raptors, but the information to be garnered could be important. For additional information on stable-isotope analyses, see Chapter 14, part C.

CONCLUSIONS

We cannot overemphasize that high-quality food-habits data are obtainable only with a correspondingly large investment of time, effort, and resources. Standardization (as much as is possible under field conditions) of data collection methods is highly desirable in order to make results comparable with other studies, and reporting of methods and results must include sufficient detail so that a study can be evaluated and compared with others. We emphasize that no matter how highly technical and sophisticated community analyses become, they will still depend on rather low-technology tools such as the ones discussed above. In other words, unless data are collected and analyzed in an unbiased manner, subsequent sophisticated analyses will not produce valid results.

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Appendix 1. Sample calculations of diversity and evenness indexes for a hypothetical raptor diet and calculation of overlap between two hypothetical raptor diets.

Diet A (raptor *j*)

	Prey species	Prey abundance	Relative abundance
	(n_i)	(p_i)	$\log_e p_i$
A	105	0.40	-0.91
B	98	0.37	-0.99
C	32	0.12	-2.09
D	25	0.10	-2.34
E	1	0.004	-5.52
Totals	261	1.00	—

Diet B (raptor *k*)

	Prey species	Prey abundance	Relative abundance
	(n_i)	(p_i)	$\log_e p_i$
A	52	0.18	-1.73
B	40	0.14	-1.99
C	115	0.39	-0.94
D	87	0.30	-2.34
E	0	0.0	-1.22
Totals	294	1.00	—

Calculation of diet diversity

Diet diversity (food-niche breadth) for the data in diet A according to the reciprocal of Simpson's Index:

$D = 1/\Sigma p_i^2$
$= 1/((0.402)^2 + (0.375)^2 + (0.123)^2 + (0.096)^2 + (0.004)^2)$
$= 1/(0.162 + 0.141 + 0.015 + 0.009 + 0.00002)$
$= 1/0.33$
$= 3.03$

Diet diversity (food-niche breadth) for the data in diet A according to Shannon's Index:

$H' = - \Sigma p_i \log p_i$
$= - [(0.402 \log 0.402) + (0.375 \log 0.375) + (0.123 \log 0.123) +$
$(0.096 \log 0.096) + (0.004 \log 0.004)]$
$= - [(0.402 (-0.911)) + (0.375 (- 0.994)) + (0.123 (-2.095)) +$
$(0.096 (-2.343)) + (0.004 -5.521))]$
$= - [-0.366 - .0373 - 0.258 - 0.225 - 0.022]$
$= 1.24$

Calculation of diet evenness

Diet evenness for the data in diet A according to Pielou's Index:

$J' H' / H max'$
$= 1.24 / H max'$
$= 1.24 / 1.609$
$= 0.77$

Diet evenness for the data in diet A according to Alatalo's modification of Hill's Index:

$F = (N_2 - 1) / (N_1 - 1)$
$= (1/D - 1) / (\text{antilog } H' - 1)$
$= (1/0.327 - 1) / (3.45 - 1)$
$= 2.06 / 2.45$
$= 0.84$

Calculation of diet overlap

Diet overlap between diets A and B according to Piankas' Index:
$O = \Sigma p_{ij} p_{ik} / \sqrt{(\Sigma pij^2, \Sigma pik^2)}$
$= ((0.40 \times 0.18) + (0.37 \times 0.14) + (0.12 \times 0.39) + (0.1 \times 0.3) + (0.004 \times 0)) /$
$\sqrt{((0.16 + 0.14 + 0.01 + 0.01 + 0.00002) \times (0.03 + 0.02 + 0.15 + 0.09))}$
$= (0.07 + 0.05 + 0.5 + 0.03) / \sqrt{(0.33 \times 0.29)}$
$= 0.2 / 0.09$
$= 0.2 / 0.31$
$= 0.64$
$0.64 \times 100 = 64\%$ overlap in diet

Appendix 2. Diet samples to illustrate calculation of diversity, evenness, and diet overlap.

Population A (simulated)

Species	Number of individuals
1	200
2	200
3	200
4	200
5	200

Species richness = 5
Diet diversity = 5.0 (1/D)
Number of individuals in population = 1,000

Population B (simulated)

Species	Number of individuals
1	100
2	100
3	100
4	100
5	100
6	100
7	100
8	100
9	100
10	100

Species richness = 10
Diet diversity = 10.0 (1/D)
Number of individuals in population = 1,000

Population C (actual diet information from Utah Barn Owls [*Tyto alba*])

Species	Number of individuals
Sorex vagrans	4,223
Eptesicus fuscus	7
Myotis spp.	8
Sylvilagus nuttalli	3
Thomomys talpoides	649
Perognathus parvus	2
Reithrodontomys megalotis	6,517
Peromyscus maniculatus	6,853
Microtus montanus	41,527
Microtus pennsylvanicus	42,718
Ondatra zibethicus	40
Rattus norvegicus	308
Mus musculus	6,193
Mustela frenata	1
Rallus limicola	4
Porzana carolina	76
Charadrius vociferus	1
Recurvirostra americana	1
Gallinago gallinago	16
Columba livia	23
Tyto alba	1
Cistothorus palustris	36
Sturnus vulgaris	382
Sturnella neglecta	11
unidentified icterid	198
Passer domesticus	146
unidentified medium passerine	455
unidentified small passerine	603
unidentified insect	14

Species richness = 29
Diet diversity = 3.33 (1/D)
Number of individuals in population = 111,016


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