

Biases in population diet studies due to sampling in heterogeneous environments: a case study with the Eagle Owl

Vincenzo Penteriani,^{1,3} Fabrizio Sergio,¹ Maria del Mar Delgado,¹ Max Gallardo,² and Miguel Ferrer¹

¹ Department of Applied Biology, Estación Biológica de Doñana, C.S.I.C., Avda. de María Luisa s/n., Pabellón del Perú, Apdo. 1056, 41013 Seville, Spain

² Parc Naturel Régional du Luberon, 60 Place Jean Jaurès, BP 122, 84404 APT, France

Received 12 August 2004; accepted 18 October 2004

ABSTRACT. Many studies have reported variation in bird diet composition related to spatial variation in habitat quality and landscape heterogeneity. Most diet analyses involve collection of food items at a sub-sample of available sites. Because individuals at different sites may vary in their diet composition, the description of the diet of a population may depend on which sites are sampled. This potential bias associated with environmental heterogeneity has never been explicitly tested. We used dietary data from a long-term study of an owl population to simulate various scenarios of diet assessment in which the investigator samples food items from various sites without taking into account their variation in quality. The simulations showed that assessment of diet composition was highly dependent on the number and type of sites sampled for food items and that such bias caused by environmental heterogeneity disappeared when food samples were randomly collected at more than 60% of the available sites. Biases in diet description may affect a large number of studies, especially of territorial species in heterogeneous landscapes. Similar biases may apply to the assessment of demographic parameters.

SINOPSIS. Sesgo en estudios sobre dietas a razón de muestreo en ambientes heterogéneos: un estudio de un caso en *Bubo bubo*

Muchos estudios han informado variaciones en la dieta relacionados con variaciones espaciales en la calidad del hábitat y lo heterogéneo del medio ambiente. La mayoría de las dietas envuelven el coleccionar artículos alimentarios y sub-muestras en armonía con los sitios de muestreo disponibles. Dado el caso de que individuos en diferentes localidades pueden variar su dieta, la descripción de la dieta de una población pudiera depender del tipo de localidad muestreada. Este sesgo asociado a heterogeneidad nunca ha sido puesto a prueba. Utilizamos los datos tomados, en un estudio de varios años, sobre la dieta de *Bubo bubo* para simular varios escenarios de la evaluación de la dieta en donde el investigador hubiera tomado datos de diferentes localidades, sin tomar en consideración la variación en la calidad del ambiente. Las simulaciones mostraron que la evaluación de la composición de una dieta depende mayormente, del número y tipos de lugares muestreados y que dicho sesgo, causado por la heterogeneidad del medio ambiente, desaparecía cuando las muestras se tomaban al azar en más del 60% de los lugares disponibles. Sesgo en la descripción de la dieta de un ave pudiera afectar muchos estudios que se han hecho, en particular con especies que viven en ambientes heterogéneos. Sesgos similares pudieran aplicar a la evaluación de parámetros demográficos.

Key words: bias in diet studies, *Bubo bubo*, Eagle Owl, habitat heterogeneity, population structure, sample size

Variation in diet composition among individuals of a population is common and may reflect individual specialization or differential habitat availability (van Valen 1965) and hence food availability. Because most landscapes are spatially heterogeneous (Wiens 1976; Forman 1995), significant ecological and management implications may arise from the relationship between habitat availability and individual variation in diet composition. In heterogeneous en-

vironments, the spatial distribution of resources around breeding sites may influence habitat selection, density, demographic parameters, and population dynamics (Holt 1985; Morris 1988; Ferrer and Donazar 1996; Both 1998; Penteriani et al. 2001, 2002). In particular, territorial and solitary-breeding species are usually considered as site-dependent (Rodenhouse et al. 1997, 1999), as their life history is tightly linked to the distribution of resources available inside their territories. Under this scenario, if individuals of a population occupy territories that differ in landscape structure and composition, and

³ Corresponding author. Email: penteriani@ebd.csic.es

if they experience habitat-specific demographic rates, then the landscape features become the major determinants of population-level processes (Ostfeld et al. 1985; Pulliam 1988; McPeck et al. 2001).

Although many authors have emphasized the importance of habitat heterogeneity (Wiens 1976; Turner 1989; Ferrer and Donazar 1996), its effect on population structure (Rosenzweig and Abramsky 1980; Ostfeld et al. 1985; Dobson and Oli 2001; Ferrer and Penteriani 2003), and individual variation in diet (Zerba and Collins 1992; Stockhoff 1993; Hupp et al. 1996), the potential impact of environmental heterogeneity on diet assessment has not been explicitly examined to our knowledge. To date, investigations of the biases potentially affecting dietary studies have mainly focused on methods of diet assessment (e.g., analysis of food remains versus direct observation of food consumption; Collopy 1983; Sheeley and Smith 1989; Rosenberg and Cooper 1990; Simmons et al. 1991; Real 1996; Marchesi et al. 2002) and digestion rates and digestibility of food items (Swanson and Bartonek 1970; Custer and Pitelka 1975; Liffield 1983; Orr and Harvey 2001). However, concern has been expressed about the consequences of individual variation in food exploitation on diet assessment and on the need to consider it in any study (Strauss 1982; Morse 1990; García-Berthou 1999). Here, we employ data from a long-term study of an owl species to demonstrate such a bias. We show that, when resources are unevenly distributed over the landscape and/or unequally available to all breeders, the emergent picture of population-level diet composition is highly dependent on which territories are sampled for diet assessment.

METHODS

Study area. Diet composition of an Eagle Owl (*Bubo bubo*) population was assessed on the basis of material collected at 27 breeding sites from 1971 to 1999 at a Mediterranean mountain in southern France (Luberon, Provence region). Detailed information on the methods employed to collect and analyze prey items are available in Penteriani et al. (2002). The study area is located in the Humid Mediterranean climate region (Donazar 1987). Elevation ranged from 160 to 700 m. Along a ver-

tical gradient within the study area, it was possible to identify two successive horizontal levels spaced 2–4 km apart (i.e., the border and the interior of the massif, with a difference in altitude of only 300 m), with clear differences in morphology, landscape structure, and land-use patterns (Penteriani et al. 2001, 2002). The border areas corresponded to the mountain piedmont and the Durance river valley, which are characterized by intense human activities. The landscape mainly consisted of open areas (i.e., croplands, pastures, and fallow lands) along the riverside and, near the border of the massif, of Mediterranean forests (*Quercus ilex*, *Q. pubescens*, and *Pinus halepensis*) and some shrubland patches, interspersed with several isolated small cliffs. The interior areas were more “natural” valleys with a mosaic structure of large rocky canyons, overhanging shrublands (mainly *Quercus coccifera*, *Thymus vulgaris*, and *Rosmarinus officinalis*) and Mediterranean forests. Decreasing grazing pressure combined with abandonment of agricultural uplands favored the development of Mediterranean forests with a corresponding reduction of open habitats (main hunting habitat of Eagle Owls; Penteriani 1996) and landscape diversity principally in the interior of the massif. Moreover, and especially in the interior of the massif, the reduction of open landscapes took place at the same time as a rapid decline in rabbits (*Oryctolagus cuniculus*) due to myxomatosis (Penteriani et al. 2001).

Study species. The Eagle Owl, the largest owl in the world (1500–3500 g), is widely distributed across Europe, Asia, and North Africa (Mikkola 1994; Penteriani 1996). It occurs in a variety of habitats, ranging from boreal forests to Mediterranean scrubland and steppes, including rocky and sandy deserts (Mikkola 1994; Penteriani 1996). Although it is one of the most specialized rabbit predators among large European raptors (Delibes and Hiraldo 1979), reaching its peak densities in those portions of the Mediterranean region in which rabbits are homogeneously distributed at high densities (Donazar 1987), its diet includes many differently sized prey species (Penteriani 1996).

Previous information on Eagle Owl diet in the study area. During the study period, all territories were sampled in all years to avoid a bias associated with possible temporal variation in diet. Previous analyses showed spatial

stability in the environmental conditions surrounding nest sites (Penteriani et al. 2004) and remarkable variation in diet composition among Eagle Owl territories due to habitat heterogeneity (Penteriani et al. 2002).

We determined diet by repeated nest visits to collect prey remains and pellets and by direct observations at sunset and sunrise. The combination of different methods to determine diet may yield more accurate estimates of the overall diet than using just one method (Rosenberg and Cooper 1990; Simmons et al. 1991). Prey remains and pellets were identified by macroscopic comparison with reference collections. We estimated live biomass by using direct measurements, mass data from the study area, and bibliographic sources (Géroudet 1946–1957). The contribution of each prey group to overall biomass was calculated by multiplying the proportion of each group by the mean body mass of individuals in the group. We pooled pellets from individual visits into a single sample for analysis. The presence of different prey types in the samples was recorded, but no attempt was made to quantify the number of individuals. To avoid duplication of prey, i.e., in remains and pellets, items found in pellets were used only if they had not been found as remains during the same visit (Penteriani 1997). By analyzing the total 2149 collected prey items, we previously demonstrated (Table 1, Penteriani et al. 2001, 2002) that richness of prey taxa in the diet of each pair (number of identified prey species; Magurran 1988) was negatively correlated with the distance to the massif border; the percentage occurrence of birds, mammals, and fish varied significantly between border and interior ($N = 9$) areas (Table 1); the Shannon index of diet diversity was significantly higher for birds along the border ($H' = 2.325$) than in interior regions ($H' = 1.935$); and a predictive model obtained through a discriminant function analysis could correctly classify all border and interior nest-sites on the basis of diet composition. Such a model was based on seven explanatory variables: the Shannon index of diet diversity and the percentage occurrence by mass of whole birds, corvids, mammals, rabbits, rats (*Rattus* sp.), and fish. Further evidence of spatial variation in diet was shown by the significant effect of diet composition of individual territories on nest spacing, laying date, and productivity (Penteriani et al. 2002). These results

demonstrated that the study population was spatially structured and composed of two types of territories: high- and low-quality ones, corresponding to border and interior nesting sites, respectively (Penteriani et al. 2002).

Statistical analyses. We created several different subsets of the entire data set to simulate different scenarios under which a hypothetical researcher might have assessed the diet composition of this population without taking into consideration its spatial structure. In particular, we employed a sequential procedure of progressive sub-sample re-arrangement and analysis. At each successive step of the procedure, we extracted 10 random combinations of different percentages of the total sample of 27 territories (see examples below). Each of these 10 random samples, hereafter defined as “extracted samples,” represents one hypothetical description of the diet composition of the population, based on an a priori arbitrarily defined subset of the overall 27 territories. The simulation represented a sampling for diet composition of only a random subset of the overall territories in the population. If environmental heterogeneity does not bias diet description, then we would expect the diet composition of the 10 extracted samples not to differ from each other (null hypothesis).

In the first step of the procedure, we randomly sampled 40% of the original 27 territories (i.e., 11 territories and their associated batches of prey items) 10 different times. At each successive step of the procedure, we randomly added 10% of the overall territories, until the difference among the diet descriptions was not significant (consequently identifying the threshold beyond which the habitat heterogeneity effect disappear). For example, in the second step of the procedure we randomly sampled 50% of the 27 territories 10 different times; in the third step we randomly sampled 60% of the 27 territories 10 different times.

At each successive step, and for each of the 10 different samples, we described diet composition for the following 10 variables, following Penteriani et al. (2002): diet richness, Shannon index of diet diversity, and percentage occurrence by mass of birds, mammals, fish, pigeons and doves, crows, hedgehogs (*Erinaceus europaeus*), rabbits, and rats. At each step of the procedure, we compared the mean values of these variables among the 10 extracted samples.

Table 1. Diet of the Eagle Owl in southern France (Luberon massif), based on 2149 items collected at 27 nest sites and identified at the species or genus level, showing percentage occurrence of prey categories by number (n%) and mass (m%) in border (18 nest sites, 1330 items) and interior (nine nest sites, 819 items) territories. Taxonomic groups accounting for less than 1% of the total prey items are not shown.

Prey	Border diet		Interior diet	
	n%	m%	n%	m%
Birds	29.5	12.6	17.2	9.0
herons, egrets and bitterns	1.0	1.8	0.0	0.0
Red-legged Partridge (<i>Alectoris rufa</i>)	1.3	1.7	1.5	1.3
pheasants	2.1	4.3	1.5	1.3
Moorhen (<i>Gallinula chloropus</i>)	1.8	1.3	1.0	0.5
<i>Columba</i> spp.	1.6	1.9	1.0	0.8
pigeons and doves	2.9	3.5	1.5	1.3
owls	1.3	1.3	1.6	1.1
Common Swift (<i>Apus apus</i>)	2.7	0.2	0.2	0.02
Alpine Swift (<i>Apus melba</i>)	1.0	0.08	0.1	0.01
swifts	3.6	0.3	0.3	0.03
Song Thrush (<i>Turdus philomelos</i>)	0.6	0.8	0.0	0.0
<i>Turdus</i> spp.	0.6	0.3	2.1	0.4
thrushes	2.7	1.3	3.2	0.7
unidentified <i>Passeriformes</i>	1.8	0.0	0.0	0.0
Magpie (<i>Pica pica</i>)	3.1	1.9	2.2	1.0
Jay (<i>Garrulus glandarius</i>)	0.3	0.1	1.5	0.5
Jackdaw (<i>Corvus monedula</i>)	2.0	1.4	1.0	0.5
unidentified <i>Corvidae</i>	1.6	0.0	0.1	0.0
crows	7.6	4.6	5.6	3.2
Mammals	61.0	65.5	80.9	88.3
hedgehog (<i>Erinaceus europaeus</i>)	5.1	13.7	8.2	16.3
brown hare (<i>Lepus capensis</i>)	0.0	0.0	1.2	6.5
rabbit (<i>Oryctolagus cuniculus</i>)	5.1	14.6	13.5	29.3
red squirrel (<i>Sciurus vulgaris</i>)	1.0	0.8	2.6	1.6
edible dormouse (<i>Glis glis</i>)	4.2	1.4	5.8	1.5
water vole (<i>Arvicola sapidus</i>)	4.9	2.8	0.0	0.0
<i>Mus</i> spp.	5.6	0.2	2.6	0.05
brown rat (<i>Rattus norvegicus</i>)	17.4	19.8	29.4	25
black rat (<i>Rattus rattus</i>)	9.5	5.4	4.3	1.8
<i>Rattus</i> spp.	2.9	2.0	9.0	4.6
rats	29.8	27.1	42.7	31.4
coypu (<i>Myocastor coypus</i>)	0.5	1.1	0.0	0.0
<i>Felis</i> spp.	0.5	2.2	0.4	1.2
Fish	7.6	9.9	1.7	1.2
<i>Leuciscus</i> spp.	0.9	2.9	0.0	0.0
<i>Cyprinus</i> spp.	6.2	6.2	1.6	1.1

Because most variables were not normally distributed (even after data-transformation), differences were tested using a Kruskal-Wallis test (Hollander and Wolfe 1973). When multiple comparisons were carried out on a set of values, the sequential Bonferroni correction was used to adjust the significance level (Rice 1989). Statistical significance was set at $P < 0.05$.

RESULTS

When comparing the 10 extracted samples, each representing a random 40% of the whole sample, we obtained significant differences among territories for all 10 variables: percentage by mass of birds ($H = 31.9$, $P = 0.0001$), mammals ($H = 31.8$, $P = 0.0001$), fish ($H =$

24.5, $P = 0.004$), pigeons and doves ($H = 25.6$, $P = 0.002$), crows ($H = 21.6$, $P = 0.010$), hedgehogs ($H = 26.4$, $P = 0.002$), rabbits ($H = 35.7$, $P = 0.0001$), rats ($H = 25.1$, $P = 0.003$), diet richness ($H = 25.0$, $P = 0.003$) and Shannon index of diet diversity ($H = 21.3$, $P = 0.011$). At the second step of the procedure, when comparing the 10 extracted samples each representing a random 50% ($N = 14$) of the whole sample, we still obtained significant differences for three of the 10 variables: percentage by mass of mammals ($H = 20.5$, $P = 0.015$), rabbits ($H = 19.0$, $P = 0.025$) and rats ($H = 22.4$, $P = 0.05$). Furthermore, the percentage by mass of birds neared the significance level ($H = 16.2$, $P = 0.06$). Finally, when the threshold of 60% ($N = 16$) of the whole sample was reached at the third step of the procedure, we did not obtain significant differences for any of the 10 variables.

DISCUSSION

Incorporating landscape heterogeneity in our population analyses led to the recognition of the existence of high- and low-quality territories, containing a differential amount of prey species and biomass (Penteriani et al. 2002, 2004). This resulted in pronounced variation in diet composition among territories. As a consequence, diet description in this population was highly context-sensitive and depended on the type and number of territories at which prey items were collected. Such results point out habitat heterogeneity as a fundamental factor to be considered in dietary studies. To our knowledge, this is the first evidence that the heterogeneous distribution of trophic resources, a consequence of habitat heterogeneity, can affect diet description.

Our study was in an area with a highly heterogeneous environment, where the border and interior areas had a fairly sharp delineation. However, variation in the characteristics of territories exists to some degrees in all natural animal populations, and can be substantial (Rodenhause et al. 1997, 1999). Therefore, we believe that our results may apply to studies in habitats that are less obviously heterogeneous. Our results also show that the potential bias associated with habitat heterogeneity may be controlled through adequate sampling. For example, in our simulated samples, the hypothet-

ical diet descriptions were not significantly different from each other after we reached a threshold of 60% of territories. Therefore, in our case study, collection of prey items at a randomly chosen sub-sample equal to at least 60% of the overall 27 territories would have been sufficient to prevent the potential bias caused by habitat heterogeneity.

Landscape heterogeneity is pronounced in most Mediterranean habitats of Europe, due to the long history of human alteration and to changes in land-use practices that occurred in the last century (Blondel et al. 1993; Naveh and Liebermann 1994; Blondel and Aronson 1999). This could have exaggerated the patterns observed in our study. However, we believe that the bias reported here could affect dietary studies conducted in other areas and on other species for three reasons. First, many regions of the world show levels of landscape heterogeneity comparable to that of the Mediterranean regions of southern Europe (Forman 1995). Second, the populations of many territorial species are known to be regulated through site-dependence, involving spatially structured populations with pronounced variation in territory quality (Rodenhause et al. 1997, 1999; McPeck et al. 2001). In these conditions, individuals are faced with an unequal availability of different prey communities, with consequently marked spatial variation in diet composition. Third, many studies have reported an association between spatial variation in diet composition and variation in breeding success (e.g., Viñuela and Veiga 1992; Arroyo 1998; Penteriani et al. 2002; Sergio et al. 2003a).

Because animal populations are complex systems composed of sub-units with high intrinsic variance among them (Ferrer and Donazar 1996; Penteriani et al. 2004), this spatial structure needs to be incorporated in analyses of diet composition. Foraging behavior represents a complex series of consecutive decisions and interactions that will be affected by spatio-temporal variation in resource availability (Stephens and Krebs 1986; Johnson et al. 2001). As a result, prey items are "a snapshot" of a composite series of behavioral decisions, hunting attempts, and interactions with biotic and abiotic factors. Diet investigations should not be carried out in isolation, but integrated into a wider population study and supported by previous

knowledge of the spatial structure and life history of the study population.

Assessing diet composition is often fundamental in wildlife management, such as when assessing the impact of a predator on a conservation-sensitive prey species (e.g. Sergio et al. 2003b) or on a species harvested by humans (e.g., Redpath and Thirgood 1997). Our results indicate that researchers should have knowledge of the spatial structure of their study population before planning an investigation of diet composition: "blind" sampling may lead to biased diet descriptions. However, in most cases, information on the spatial structure of the study population will not be available, as, for example, in analyses of stomach contents of dead individuals not associated with a population study, or at the start of a study.

When information on spatial structure is or is not available, in either case we recommend (1) sampling food items either at all available sites, or through random sampling at as many sites as possible, ensuring that such sites are randomly chosen and not opportunistically sampled based, for example, on accessibility; and (2) collecting or retaining for analysis an equal number of food items at each site. When information on spatial variation in site quality is not available, the analysis of a similar as possible number of food items for each site may reduce the effective sample size. We recognize, however, that researchers may want to employ all the available data, especially when working on rare, or highly threatened species studied during difficult field expeditions. In such cases, we suggest reporting diet composition by pooling data from all sampled sites and showing the cumulative percentage for each food type, as in Table 1, and by calculating the percentage occurrence of each food type within the sample collected at each site and reporting the average occurrence (\pm some measure of variation) of each food type across sites.

In conclusion, in heterogeneous landscapes the description of the diet of a population may depend on which sites are sampled, leading to subtle biases in diet assessment. Such biases are likely to be widespread and may apply not just to dietary investigations but also to other studies in which the researcher samples a subset of the available sites that vary spatially.

ACKNOWLEDGMENTS

We are indebted to D. E. Andersen, B. Arroyo, P. H. Bloom, C. and P. Horisberger, H. Magnin, R. W. Mannan, and two anonymous referees for their help at various stages of the study and for comments. P. Bayle, G. Marangoni, P. Orsini, and E. Violet helped with prey identification. V. Penteriani was supported by grants from the Regional Park of Luberon (France) and from the Consejo Superior de Investigaciones Científicas (C.S.I.C., Spain).

LITERATURE CITED

- ARROYO, B. E. 1998. Effect of diet on the reproductive success of Montague's Harrier *Circus pygargus*. *Ibis* 140: 690–693.
- BLONDEL, J., P. C. DIAS, M. MAISTRE, AND P. PERRET. 1993. Habitat heterogeneity and life-history variation of Mediterranean Blue Tits (*Parus caeruleus*). *Auk* 110: 511–520.
- , AND J. ARONSON. 1999. *Biology and wildlife of the Mediterranean region*. Oxford University Press, Oxford, UK.
- BOTH, C. 1998. Density dependence of clutch size: habitat heterogeneity or individual adjustment? *Journal of Animal Ecology* 67: 659–666.
- COLLOPY, M. W. 1983. A comparison of direct observations and collections of prey remains in determining the diet of Golden Eagles. *Journal of Wildlife Management* 47: 360–368.
- CUSTER, T. W., AND F. A. PITELKA. 1975. Correction factors for digestion rates for prey taken by Snow Buntings (*Plectrophenax nivalis*). *Condor* 77: 210–212.
- DELIBES, M., AND F. HIRALDO. 1979. The rabbit as prey in the Iberian Mediterranean ecosystem. *Proceedings of the World Lagomorph Conference*, pp. 614–622.
- DOBSON, F. S., AND M. K. OLI. 2001. The demographic basis of population regulation in Columbian ground squirrels. *American Naturalist* 158: 236–247.
- DONÁZAR, J. A. 1987. Geographic variation in the diet of Eagle Owls in western Mediterranean Europe. In: *Biology and conservation of northern forest owls: symposium proceedings* (R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, eds.), pp. 220–224. U.S. Forest Service General Technical Report RM 142, Fort Collins, CO.
- FERRER, M., AND J. A. DONÁZAR. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77: 69–74.
- , AND V. PENTERIANI. 2003. A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Animal Behaviour* 66: 137–143.
- FORMAN, R. T. T. 1995. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- GARCÍA-BERTHOUE, E. 1999. Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins

- within a lake. *Archives of Hydrobiology* 146: 239–256.
- GEROUDET, P. 1946–1957. *La vie des oiseaux*, vol. 1–6. Collection de Poche. Les Beautés de la Nature. Delachaux et Niestlé S. A., Paris, France.
- HOLLANDER, M., AND D. A. WOLFE. 1973. *Nonparametric statistical methods*. Wiley, New York, NY.
- HOLT, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28: 181–208.
- HUPP, J. W., R. G. WHITE, J. S. SEDINGER, AND D. G. ROBERTSON. 1996. Forage digestibility and intake by Lesser Snow Geese: effects of dominance and resource heterogeneity. *Oecologia* 108: 232–240.
- JOHNSON, C. J., K. L. PARKER, AND D. C. HEARD. 2001. Foraging across a variable landscape: behavioral decision made by woodland caribou at multiple spatial scales. *Oecologia* 127: 590–602.
- LIFJELD, J. 1983. Stomach content analyses of the Dunlin *Calidris alpina*: bias due to differential digestibility of prey items. *Cinclus* 6: 43–46.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Croom Helm, London, UK.
- MARCHESI, L., P. PEDRINI, AND F. SERGIO. 2002. Biases associated with diet study methods in the Eagle Owl. *Journal of Raptor Research* 36: 11–16.
- MCPEEK, M. A., N. L. RODENHOUSE, R. T. HOLMES, AND T. W. SHERRY. 2001. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. *Oikos* 94: 417–424.
- MIKKOLA, H. 1994. Eagle Owl. In: *Birds in Europe: their conservation status* (G. M. Tucker, and M. F. Heath, eds.), pp 326–327. BirdLife Conservation Series no. 3. Cambridge, UK.
- MORRIS, D. W. 1988. Habitat-dependent population regulation and community structure. *Evolutionary Ecology* 2: 253–269.
- MORSE, D. H. 1990. Food exploitation by birds: some current problems and future goals. *Studies in Avian Biology* 13: 134–143.
- NAVEH, Z., AND A. LIEBERMAN. 1994. *Landscape ecology. Theory and application*. 2nd ed. Springer-Verlag, New York, NY.
- ORR, A. J., AND J. T. HARVEY. 2001. Quantifying errors associated with using fecal samples to determine the diet of the California sea lion (*Zalophus californianus*). *Canadian Journal of Zoology* 79: 1080–1087.
- OSTFELD, R. S., W. Z. LIDICKER, JR., AND E. J. HESKE. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles. *Oikos* 45: 433–442.
- PENTERIANI, V. 1996. *The Eagle Owl*. Calderini Edagricole, Bologna, Italy.
- . 1997. Long-term study of a Goshawk breeding population on a Mediterranean mountain (Abruzzi Apennines, central Italy): density, breeding performances and diet. *Journal of Raptor Research* 31: 308–312.
- , M. GALLARDO, P. ROCHE, AND H. CAZASSUS. 2001. Effects of landscape spatial structure and composition on the settlement of the Eagle Owl *Bubo bubo* in a Mediterranean habitat. *Ardea* 89: 331–340.
- , ———, AND ———. 2002. Landscape structure and food supply affect Eagle Owl *Bubo bubo* density and breeding performance: a case of intra-population heterogeneity. *Journal of Zoology* 257: 365–372.
- , M. M. DELGADO, M. GALLARDO, AND M. FERRER. 2004. Spatial heterogeneity and structure of bird populations: a case example with the Eagle Owl. *Population Ecology* 46: 185–192.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.
- REAL, J. 1996. Biases in diet study methods in the Bonelli's Eagle. *Journal of Wildlife Management* 60: 632–638.
- REDPATH, S. M., AND S. J. THIRGOOD. 1997. *Birds of prey and Red Grouse: report of the joint raptor study*. Her Majesty's Stationery Office, London, UK.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223–225.
- RODENHOUSE, N. L., T. W. SHERRY, AND R. T. HOLMES. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* 78: 2025–2042.
- , ———, AND ———. 1999. Multiple mechanisms of population regulation: contributions of site dependence, crowding, and age structure. *Proceedings of the International Ornithological Congress* 22: 2939–2952.
- ROSENBERG, K. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13: 80–90.
- ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1980. Microtine cycles: the role of habitat heterogeneity. *Oikos* 34: 141–146.
- SERGIO, F., P. PEDRINI, AND L. MARCHESI. 2003a. Spatio-temporal shifts in gradients of habitat quality for an opportunist avian predator. *Ecography* 26: 243–255.
- , L. MARCHESI, AND P. PEDRINI. 2003b. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* 72: 232–245.
- SHEELEY, D. G., AND L. M. SMITH. 1989. Tests of diet and condition bias in hunter-killed Northern Pintails. *Journal of Wildlife Management* 53: 765–769.
- SIMMONS, R. E., D. M. AVERY, AND G. AVERY. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research* 25: 63–67.
- STEPHENS, D. W., AND J. R. KREBS. 1986. *Foraging theory*. Princeton University Press, Princeton, NJ.
- STOCKHOFF, B. A. 1993. Diet heterogeneity: implications for growth of a generalist herbivore, the gypsy moth. *Ecology* 74: 1939–1949.
- STRAUSS, R. E. 1982. Influence of replicated subsamples and subsample heterogeneity on the linear index of food selection. *Transactions of the American Fisheries Society* 111: 517–522.
- SWANSON, G. A., AND J. C. BARTONEK. 1970. Bias associated with food analysis in gizzards of Blue-

- winged Teal. *Journal of Wildlife Management* 34: 739–746.
- TURNER, M. G. 1989. Landscape ecology: the effect of pattern on processes. *Annual Review of Ecology and Systematics* 20: 171–197.
- VAN VALEN, L. 1965. Morphological variation and width of ecological niche. *American Naturalist* 99: 377–388.
- VIÑUELA, J., AND J. P. VEIGA. 1992. Importance of rabbits in the diet and reproductive success of Black Kites in southwestern Spain. *Ornis Scandinavica* 23: 132–138.
- WIENS, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7: 81–120.
- ZERBA, K. E., AND J. P. COLLINS. 1992. Spatial heterogeneity and individual variation in diet of an aquatic top predator. *Ecology* 73: 268–279.