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Factors Affecting Interspecies Variation in Home-range Size of Raptors

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Considerable work has been devoted to examining factors that affect interspecies variation in home-range size. Home ranges for most vertebrates increase with body mass and decrease with increased habitat productivity (e.g. McNab 1963, Schoener 1968, Harestad and Bunnell 1979, Lindstedt et al. 1986). Large species have high energetic requirements and presumably must occupy large home ranges to obtain sufficient food, but even small species occupy relatively large home ranges when the availability of food is low. Interspecific variation in home-range size also has been attributed to differences in age and sex (Harestad and Bunnell 1979, Schoener and Schoener 1982), dominance status (Schoener and Schoener 1982), and trophic status (McNab 1963, Schoener 1968). For example, McNab (1963) showed that mammalian "hunters" have larger home ranges than similar-sized "croppers" and suggested that this difference was due to less biomass of food per unit area being available at higher trophic levels.

Raptors provide valuable insights into the factors that affect an animal's home-range size because they use many different hunting tactics and take many different kinds of prey (Snyder and Wiley 1976, Marti et al. 1993, Korpimäki and Marti 1995). Newton (1979:63) has shown that home-range size of raptors increases with body mass, and Schoener (1968) has shown that predatory birds have larger home ranges than similar-sized nonpredatory birds. Here, I extend Newton's and Schoener's analyses by asking the question: Does the way in which a raptor exploits its prey base influence the size of its home range?

Assuming that raptor home ranges are determined, in part, by food availability (e.g. Marquiss and Newton 1981, Village 1982), at least four predictions can be made about the size of a raptor's home range. First, invertebrates generally occur in higher densities than mammals for a given body size, whereas mammals generally occur in higher densities than birds for a given body size (Greenwood et al. 1996, Silva et al. 1997). Hence, one would expect bird-eating raptors to have larger home ranges than mammal-eating raptors, which in turn should have larger home ranges than invertebrate-eating raptors. Second, predators specializing on a narrow prey base should have to range over a relatively large area in order to encounter sufficient prey, whereas generalists should encounter sufficient food within a smaller area (Schoener 1969). Third, "population biomass" increases with body mass for both birds and mammals (Maurer and Brown 1988, Silva et al. 1997). Therefore, one would expect raptors that consume large prey to have relatively small home ranges. Fourth, one might expect raptor home ranges to increase with latitude, as they do for mammals (Harestad and Bunnell 1979, Lindstedt et al. 1986), because primary productivity decreases with latitude (Lieth and Whitaker 1975). Alternatively, one might expect breeding-season home ranges to decrease with latitude because of a dramatic increase in primary productivity in the summer at northerly latitudes.

Methods.—For the purposes of this study, I considered raptors to be species within the orders Falconiformes and Strigiformes, excluding carrion eaters. In addition, I followed Burt's (1943) definition that a home range is the total area normally traversed by an individual during foraging, resting, reproduction, and shelter-seeking activities.

I collected estimates of home-range size, body mass, mean prey mass, diet breadth, and the proportion of mammals, birds, and invertebrates in the diet for 32 species of Holarctic raptors (Appendix). I also recorded the latitude of the study from which home-range data were obtained. If more than one estimate existed for a variable, I took the mean. Because raptor diets vary in response to geographic gradients in prey availability (Korpimäki and Marti 1995), I collected diet estimates in the following order of priority: (1) from the same study as the home-range estimate, (2) from the same geographic region as the home-range estimate, and (3) from the nearest geographic region(s) to the home-range estimate. Following Korpimäki and Marti (1995), I calculated dietary breadth at two levels of discrimination that assessed both the number of prey types and their evenness in a sample ($1/p_i^2$; Levins 1968), where p was the proportion of prey type i. At the broader level (B_{cl}), the prey types were taxonomic classes. At the finer level (B_{sp}), the prey types were represented by species and genera for vertebrates and by orders for invertebrates. Thus, a raptor could have a narrow diet based on B_{cl} but a broad diet based on B_{sp}. Because no estimate of mean prey mass existed for Flammulated Owls (*Otus flammeolus*), I used a value of 1 g because this species preys almost exclusively on insects (Goggans 1986).

Because raptor home-range size can vary by sex (Kennedy et al. 1994) and time of year (Village 1982), I used estimates only from males during the breeding season. In addition, I used studies in which conventional or satellite radio telemetry was used be-

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TABLE 1. Description of *a priori* hypotheses and linear models concerning the effect of body mass and foraging strategy on home-range size in Holarctic raptors. All models were evaluated with and without latitude as a covariate and order (Strigiformes vs. Falconiformes) as a grouping variable.

Hypothesis	Model structure[a]	Expected result
Positive effect of body mass	$\beta_0 + \beta_1(\text{BM})$	$\beta_1 > 0$
Negative effect of the proportion of mammals	$\beta_0 + \beta_1(\text{PM})$	$\beta_1 < 0$
Positive effect of the proportion of birds	$\beta_0 + \beta_1(\text{PB})$	$\beta_1 > 0$
Positive effect of body mass and negative effect of the proportion of mammals	$\beta_0 + \beta_1(\text{BM}) + \beta_2(\text{PM})$	$\beta_1 > 0$, $\beta_2 < 0$
Positive effect of body mass and positive effect of the proportion of birds	$\beta_0 + \beta_1(\text{BM}) + \beta_2(\text{PB})$	$\beta_1 > 0$, $\beta_2 > 0$
Negative effect of diet breadth	$\beta_0 + \beta_1(B_{\text{cl}})$	$\beta_1 < 0$
Negative effect of diet breadth and positive effect of body mass	$\beta_0 + \beta_1(B_{\text{cl}}) + \beta_2(\text{BM})$	$\beta_1 < 0$, $\beta_2 > 0$

[a] BM = body mass, PM = proportion of mammals in diet, PB = proportion of birds in diet, B_{cl} = diet breadth at class level.

cause home-range estimates based on visual observations are biased low (Village 1982, Baekken et al. 1987). I preferentially selected studies that used the minimum convex polygon method (Mohr 1947). These restrictions limited sample sizes in terms of the number of species and the number of home-range estimates per species, but they reduced the variation in these estimates that results from extraneous factors.

A problem with comparative studies is that individual species do not necessarily represent independent data points because they are members of the same phylogeny (Felsenstein 1985, Pagel and Harvey 1988). Therefore, I used the nested analysis of variance-allometry approach discussed by Pagel and Harvey (1988). This involved calculating the amount of variation present at each of the four levels of taxonomy (i.e. among orders, families, genera, and species) for each of the variables using a four-factor, fixed effect, nested ANOVA (SAS 1991). The taxonomic level that contained the largest amount of the overall variation in the variables was used in further statistical analyses. I then examined the correlation among predictor variables using Pearson's correlation coefficient. If $r > 0.50$ for any two variables, I considered them redundant and subjectively deleted the one I thought least likely to influence home-range size. I did not include Swallow-tailed Kites (*Elanoides forficatus*) in the variable-selection process because I was unable to locate an estimate of mean prey mass or B_{sp} for this species.

Once redundant variables were excluded, I used general linear models (SAS 1991) to estimate variation in raptor home-range size in relation to the remaining predictor variables. I considered body mass, latitude, and diet as covariates and order (Falconiformes or Strigiformes) as a grouping variable. I constructed several *a priori* hypotheses as to how predictor variables might affect home-range size based on the four predictions discussed above. Hypotheses were translated into a set of competing linear models (Table 1), which were ranked based upon their AICc values (Anderson et al. 1994, Burnham and Anderson 1998). I considered models within 2 AICc values of the top-ranked model as competing models. Using an objective model-selection criterion such as AICc has the advantage over traditional hypothesis testing in that a hypothesis is not simply rejected based upon an arbitrarily designated critical value. Home-range size and body mass were $\log_{10}$ transformed, whereas the proportions of mammals, birds, and invertebrates were square-root and then arcsine transformed for all analyses.

Results.—I retained species as the unit of measurement because it contained more variation than the other taxonomic levels for six of the nine variables, including home-range size (Table 2). Furthermore, higher taxonomic levels contained 10% or less of the

TABLE 2. Percent of variation present for nine variables at four levels of taxonomy for Holarctic raptors.

Level	Home-range size	Latitude	Body mass	% Birds	% Invertebrates	% Mammals	B_{cl}[a]	B_{sp}[b]	Mean prey mass
Order	28.2	0.0	35.2	0.0	10.5	30.2	3.3	21.0	35.6
Family	22.0	11.4	0.0	34.5	0.0	0.0	0.0	0.0	0.0
Genus	2.3	6.2	42.8	0.0	22.7	15.1	61.7	3.9	50.3
Species	47.5	82.4	22.0	65.5	66.8	54.7	35.1	75.2	14.1

[a] Diet breadth at class level.

[b] Diet breadth at species level.

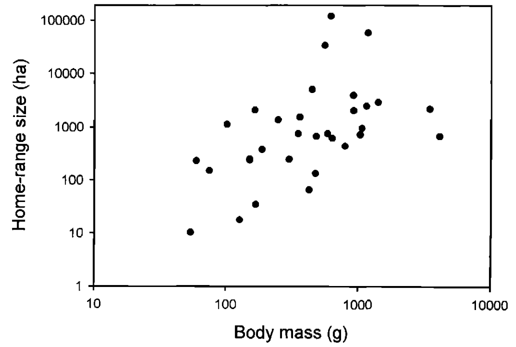

FIG. 1. The relationship between body mass and home-range size for Holarctic raptors.

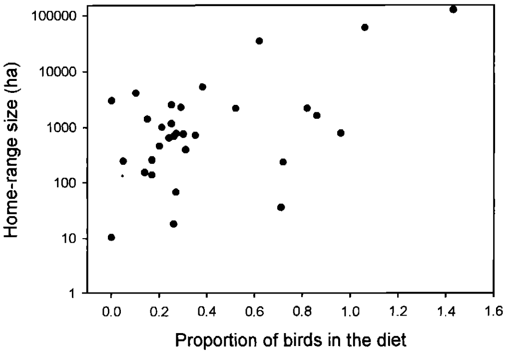

FIG. 2. The relationship between the proportion of birds in the diet (square-root then arcsine transformed) and home-range size for Holarctic raptors.

total variation for at least three variables. Mean prey mass was correlated with body mass ($r = 0.72$), B_{sp} was correlated with the proportion of birds in the diet ($r = 0.51$), and the proportion of invertebrates was negatively correlated with the proportion of mammals in the diet ($r = -0.57$). Therefore, I eliminated mean prey mass, B_{sp}, and the proportion of invertebrates in the diet from further analysis. I included Swallow-tailed Kites in the final analysis because mean prey mass and B_{sp} were no longer being considered.

The best-ranked model, which indicated that home-range size increased with increasing body mass and the proportion of birds in the diet (AICc = 90.93; Figs. 1 and 2), explained 50% of the variation in home-range size. The second best model (AICc = 91.87) included an order effect in addition to body mass and the proportion of birds in the diet. No other model was within 3 AICc units of the top model. By themselves, body mass explained 28% of the variation in home-range size, and the proportion of birds in the diet explained 27% of the variation in home-range size. Hence, each variable added reasonable amounts of explanatory power to the best model (ca. 22%). Furthermore, these two variables were uncorrelated ($r = 0.09$), indicating that they were independently important predictors of home-range size. The slope (b) of home-range size on body mass was 1.91 ± SE of 0.30 using reduced major-axis regression, which incorporates error in the independent variable (Harvey and Mace 1982). Falconiforms had numerically larger home ranges ($\bar{x}$ = 14,104.6 ± = 7751.9 ha) than strigiforms ($\bar{x}$ = 571.8 ± 175.4 ha), but because order was not in the top-ranked model, I inferred that equal-sized falconiforms and strigiforms had similar-sized home ranges.

Discussion.—At least three nonexclusive hypotheses can explain the relationship between the proportion of birds in the diet and home-range size. First, avian prey generally are less abundant than mammalian and invertebrate prey for a given body size (Maurer and Brown 1988, Greenwood et al. 1996, Silva et al. 1997). In other words, the biomass of available food within a given area should be relatively low for raptors that consume primarily birds. Marzluff et al. (1997a) found that Prairie Falcons (*Falco mexicanus*) in Idaho increased their home-range size when they switched from a diet of ground squirrels to more sparsely distributed birds and reptiles. Second, bird-eating raptors have lower encounter rates and hunting success than other raptors (Temeles 1985), which could lower the availability of avian prey in comparison to nonavian prey. Third, bird-eating raptors may be less opportunistic in diet choice than are mammal-eating raptors (Korpimäki and Marti 1995). Hence, if the abundance of primary prey is reduced, mammal-eating raptors may switch to alternative prey in the same area, whereas bird-eating raptors may need to range over a wider area to find sufficient numbers of preferred prey. Regardless of the explanation for bird-eating raptors having large home ranges, this result indicates that variation in foraging habits *within* a given trophic level (e.g. carnivores) can be as important as variation in foraging habits *among* trophic levels (e.g. carnivores vs. herbivores) when explaining variation in home-range size.

As in other vertebrate taxa, home-range size in raptors increased with body mass. Presumably, if the slopes of the home-range size/body-size regression and the energetic-requirement/body-size regression are equal, then home-range size is determined directly by metabolic needs. McNab (1963) found no difference between these slopes, but others have found that home-range size increases with body mass faster than would be expected based on energetic requirements (Schoener 1968, Harestad and Bunnell 1979, Mace and Harvey 1983). As a result, the latter workers concluded that some factor other than energetic requirements also influences home-range size. The slope relating home-range size to body mass for raptors ($b = 1.91$, SE = 0.30) in this study was significantly greater ($t = 13.6$, $P < 0.01$) than the slope of field metabolic rate on body mass for birds ($b = 0.67$, SE = 0.03) as recalculated from Nagy (1987) using reduced major-axis regression. Harestad and Bunnell (1979) hypothesized that as home-range area increases to meet the energetic requirements of larger animals, the area might encompass more and more unsuitable habitat. As a result, to acquire sufficient food resources, a large animal would need to forage over a larger area than predicted by energetic requirements alone. Indeed, Harestad and Bunnell (1979) are correct in stating that one should not expect home-range size to scale with energetic requirements independent of the distribution of food resources.

One of the goals of any comparative study should be to develop testable hypotheses for future studies. The relationship between avian prey and home-range size could be evaluated further using a conspecific population of raptors that exhibited sufficient variation in the proportion of birds in their diet, such as Northern Harriers (*Circus cyanus*), Northern Goshawks (*Accipiter gentilis*), or Prairie Falcons. Ideally, such a study would be conducted in an area that contained varying densities of birds and mammals and a mosaic of open and covered habitat types. One would then be able to evaluate the relative importance of mammalian and avian prey densities and the effect of prey catchability on home-range size.

In contrast to Harestad and Bunnell (1979) and Lindstedt et al. (1986), I found no relationship between latitude and home-range size. One explanation is that considerable variation in primary productivity exists at a given latitude owing to differences in temperature and precipitation. Examining the relationship between home-range size and productivity for single species would help explain geographic variation in home-range size by eliminating interspecific variation. Such an analysis could be conducted on the Spotted Owl (*Strix occidentalis*), whose home-range size has been estimated over a wide range of ecological conditions as well as over a large geographic and latitudinal range.

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APPENDIX. Data[a] and sources[b] for the raptor species used in this study. All data on raptor body mass are from Dunning (1993). Within orders, taxa are listed alphabetically rather than taxonomically.

Species	Home range	Lat.	Body mass	Prey mass	% Birds	% Mammals	% Inverts.	B_{sp}	B_{cl}	Source
Accipiter cooperii	764	44	349	83	0.67	0.22	0.02	16.57	1.30	35, 41, 49
Accipiter gentilis	2,106	37	912	232	0.54	0.37	0.09	18.22	1.99	29, 35, 49
Accipiter nisus	255	55	150	26	0.03	0.97	0.00	6.16	1.02	34, 35, 42
Aquila chrysaetos	2,253	43	3,447	854	0.08	0.90	0.00	4.86	1.43	7, 35, 38, 49
Buteo jamaicensis	748	38	1,028	130	0.09	0.51	0.37	16.14	2.07	1, 35, 49
Buteo lineatus	135	33	475	44	0.03	0.21	0.54	4.14	1.82	8, 27, 47, 49
Buteo regalis	990	43	1,059	179	0.04	0.85	0.10	6.59	1.40	35, 39, 49
Buteo swainsoni	4,038	37	908	63	0.01	0.04	0.94	4.74	2.90	3, 35, 49
Circus cyaneus	1,570	43	358	60	0.57	0.30	0.11	10.32	1.68	35, 36, 45, 49
Elanoides forficatus	5,107	26	442	—	0.14	0.00	0.37	—	3.78	40, 49
Haliaeetus leucocephalus	700	55	4,130	529	0.12	0.04	0.01	22.69	1.78	19, 25, 35, 49
Falco columbarius	2,133	46	163	26	0.25	0.01	0.74	13.42	1.00	5, 35, 49
Falco mexicanus	34,187	43	554	99	0.33	0.22	0.45	4.36	1.95	35, 37, 49
Falco peregrinus	122,550	39	611	150	0.98	0.00	0.02	17.47	1.01	13, 26, 35, 49
Falco rusticolus	58,900	69	1,170	372	0.76	0.24	0.00	4.11	1.54	31, 35, 46, 49
Falco tinnunculus	386	56	186	28	0.09	0.65	0.25	2.74	1.66	32, 35, 53
Pandion haliaetus	2,955	45	1,403	296	0.00	0.00	0.01	2.31	1.00	35, 44, 49, 50
Aegolius acadicus	150	66	75	22	0.02	0.98	0.01	5.47	1.05	11, 12, 35
Aegolius funereus	1,148	45	101	29	0.06	0.78	0.16	5.90	1.57	23
Asio otus	1,390	49	245	26	0.02	0.97	0.01	5.06	1.10	35, 48, 49, 52, 54
Athene cunicularia	241	52	151	3	0.00	0.07	0.91	3.00	1.76	21, 35, 49
Bubo virginianus	2,499	46	1,142	46	0.06	0.78	0.15	9.76	1.11	15, 35, 49
Glaucidium passerinum	231	59	60	17	0.43	0.56	0.00	7.42	2.04	33, 35
Otus asio	36	37	167	34	0.43	0.07	0.32	4.32	1.35	6, 18, 35
Otus flammeolus	10	45	54	1	0.00	0.00	1.00	2.46	1.64	20
Otus kennicottii	18	46	127	4	0.07	0.88	0.07	7.49	2.31	22, 35
Strix aluco	67	52	426	26	0.07	0.67	0.03	9.24	1.64	2, 28, 35
Strix occidentalis	770	36	582	51	0.07	0.85	0.07	4.85	1.39	10, 16, 17, 35, 51, 55
Strix nebulosa	450	45	789	60	0.04	0.96	0.00	3.19	1.01	9, 14, 35, 49
Strix varia	635	45	632	41	0.06	0.76	0.16	7.96	1.37	35, 43, 49
Surnia ulula	249	61	299	25	0.03	0.97	0.00	0.19	3.69	4, 30, 35, 49
Tyto alba	682	39	479	36	0.07	0.92	0.02	1.73	1.03	24, 35, 49

[a] Home range = mean home-range size (rounded to nearest ha); lat. = latitude of home-range study; body mass = mean body mass of raptor (rounded to nearest g); prey mass = mean mass of prey in diet (rounded to nearest g); % birds = % birds in diet; % mammals = % mammals in diet; % inverts. = % invertebrates in diet; B_{sp} = diet breadth by species; B_{cl} = diet breadth by class.

[b] 1 = Andersen and Rongstad (1989); 2 = Appleby (1995); 3 = Babcock (1995); 4 = Baekken et al. (1987); 5 = Becker and Sieg (1987); 6 = Belthoff et al. (1993); 7 = Bloom and Hawks (1982); 8 = Bloom et al. (1993); 9 = Bull and Henjum (1990); 10 = Call et al. (1992); 11 = Cannings (1987); 12 = Cannings (1993); 13 = Enderson and Craig (1997); 14 = Franklin (1988); 15 = Fuller (1979); 16 = Ganey (1992); 17 = Ganey and Balda (1989); 18 = Gelbach (1994); 19 = Gerrard et al. (1992); 20 = Goggans (1986); 21 = Haug and Oliphant (1990); 22 = Hayward (1983); 23 = Hayward et al. (1993); 24 = Hegdal and Blaskiewicz (1984); 25 = Hunt et al. (1992); 26 = Hunter et al. (1988); 27 = Jaksić and Carothers (1985); 28 = Jędrzejewski et al. (1994); 29 = Kennedy et al. (1994); 30 = Kertell (1986); 31 = Klugman et al. (1993); 32 = Korpimäki (1985); 33 = Kullberg (1995); 34 = Marquiss and Newton (1981); 35 = Marti et al. (1993); 36 = Martin (1987); 37 = Marzluff et al. (1997a); 38 = Marzluff et al. (1997b); 39 = McAnnis (1990); 40 = Meyer and Collopy (1990); 41 = Murphy et al. (1988); 42 = Newton and Marquiss (1982); 43 = Nicholls and Fuller (1987); 44 = Phelps (1993); 45 = Picozzi (1978); 46 = Poole and Boag (1988); 47 = Portnoy and Dodge (1979); 48 = L. Powers pers. comm.; 49 = Snyder and Wiley (1976); 50 = Swenson (1978); 51 = Thraikill and Bias (1989); 52 = Thurow and White (1984); 53 = Village (1982); 54 = Wijnandts (1984); 55 = Zwank et al. (1994).