

NOTES AND COMMENTS

POPULATION DENSITY AND BODY SIZE IN BIRDS

The prediction of animal abundance from one or a few independent variables is a fundamental goal in ecology (Andrewartha 1961). One characteristic that may permit such predictions is animal size. An inverse relationship between body size and population density has been demonstrated for a variety of animals (Elton 1966; Clutton-Brock and Harvey 1977; Damuth 1981; Rimmert 1981; Peters 1983; Peters and Raelson 1984).

Peters and Wassenberg (1983) showed that the relationship was consistent in all animals except birds. However, almost all their bird data were obtained from only one source (Emlen 1972), a wintering bird population in a small study site in southern Texas. Only 60 points were included, thus producing a limited size range. Newton (1979) found that density was negatively correlated with body size in birds of prey and was associated with their feeding habits.

In light of this confusion concerning the effect of body size on avian densities, this study has two objectives: to reexamine the relationship of body size and density in birds by using data from many species within different areas and over a large range of body weights, and to classify these data by feeding type and habitat to test whether the relationship depends on food resources.

The data were collected from an extensive literature survey. Values for numerical bird density were extracted from 13 sources, creating 29 data sets stratified by area and habitat (table 1). The original densities were converted to the chosen standard, the number of birds per square kilometer. Thus, when the density was given in pairs per unit area, the value was doubled to make it birds per unit area, and the units of area were converted to square kilometers. Densities originally given in males per unit area were also doubled because I assumed that there was a female for every male present. This assumption is probably valid because most of the censuses enumerated singing males during breeding periods. Although the presence of unmated and drifter males may cause some underestimation, this error is probably small since most insectivorous and carnivorous species tend toward monogamy and their overall sex ratios are close to unity (Welty 1982). Additionally, the effect of any error would be spread consistently over the whole range of body sizes, thus not affecting the precision of any prediction.

Previous studies (Andrewartha 1961; Armstrong 1965; Lack 1966; Schoener

TABLE 1
DESCRIPTION OF DATA SETS AND RANGES OF BODY WEIGHTS (G) FOR FOUR DIETARY CATEGORIES OF BIRDS

CHARACTERISTICS AND LOCATION	MEASURE OF DENSITY	FEEDING TYPE*					RANGE	SOURCE	
		IN	HE	OM	RP	Total			
Breeding birds of the forest edge in Illinois	pairs/60 acres	22	3	1	1	1	27	3.0-504.0	Johnston 1947
Breeding birds of Portage bog, southwestern Michigan	males/100 acres	12	3	2	0	0	17	3.0-130.0	Brewer 1967
Breeding birds of Sugarloaf bog, southwestern Michigan	males/100 acres	16	0	3	0	0	19	9.7-130.0	Brewer 1967
Birds on various coast-forest census plots, B.C.	males/km ²	9	1	1	0	0	11	3.3-88.0	Buckner et al. 1975
Breeding birds in western hemlock stands, Port Alice, B.C.	males/km ²	14	2	3	0	0	19	3.3-637.0	Buckner et al. 1975
Breeding birds of burned plots in conifer forests, Sierra Nevada	pairs/100 acres	18	6	2	0	0	26	8.0-145.0	Bock & Lynch 1970
Same area, unburned plots	pairs/100 acres	16	4	3	0	0	23	5.0-145.0†	Bock & Lynch 1970
Birds in various vegetation communities in Yukon	males/40 ha	27	6	2	2	2	37	6.7-680.0†	Theberge 1976
Breeding birds in 2 Arizona woods, foliage nesters	pairs/100 acres	10	5	2	0	0	17	3.2-125.0	Balda 1970
Same area, cavity and ground nesters	pairs/100 acres	6	3	1	1	1	11	18.0-800.0	Balda 1970
Nesting birds of the river-bottom forests, Oklahoma	pairs/100 acres	29	2	1	2	2	34	3.0-680.0†	Carter 1967
Nesting birds of the stream-bottom forests, Oklahoma	pairs/100 acres	20	2	2	3	2	27	3.0-450.0†	Carter 1967

Nesting birds of the upland forests, Oklahoma	pairs/100 acres	19	0	2	1	22	6.7–112.0	Carter 1967
Most abundant birds on cultivated land in northwestern Germany	pairs/635 km ²	3	1	2	0	6	18.5–45.0	Oelke 1966
Breeding birds on sagebrush-grassland in central Montana	pairs/100 acres	3	2	0	0	5	11.0–87.5	Feist 1968
Waterfowl in Utah	pairs/200 acres	2	8	0	0	10	315.0–1320.5	Ryder 1959
Urban areas, boreal Canada	males/km ²	14	3	6	0	23	10.5–139.0†	Erskine 1977
Bogs and dens, boreal Canada	males/km ²	17	2	3	0	22	6.7–1134.0	Erskine 1977
Poplar or birch, boreal Canada	males/km ²	9	0	1	0	10	8.1–533.3	Erskine 1977
Western coniferous forests, boreal Canada	males/km ²	15	0	1	0	16	6.1–533.3	Erskine 1977
Tamarack forests, boreal Canada	males/km ²	11	0	1	0	12	6.1–533.3	Erskine 1977
Jack, lodgepole pines, boreal Canada	males/km ²	8	0	0	0	8	6.7–84.5	Erskine 1977
Jack pines, boreal Canada	males/km ²	15	0	1	0	16	6.1–84.5	Erskine 1977
White, red pitch pine, boreal Canada	males/km ²	7	0	1	0	8	10.5–533.3	Erskine 1977
Hemlock stands, boreal Canada	males/km ²	17	0	1	0	18	6.1–533.3	Erskine 1977
Balsam, fir stands, boreal Canada	males/km ²	18	0	1	0	19	6.1–84.5	Erskine 1977
Spruce stands, boreal Canada	males/km ²	23	0	3	0	26	6.1–533.3†	Erskine 1977
Large raptors in northeastern Colorado	pairs/100 km ²	0	0	0	5	5	262.5–4536.0	Olendorff 1975
Raptors of the Seward peninsula, Alaska	pairs/5700 km ²	0	0	0	4	4	964.0–4536.0	Swartz et al. 1975

* IN, insectivores; HE, herbivores; OM, omnivores; RP, raptors.

† Sets that produced significant regressions.

1968; King 1970) have shown that the variation in population density for different species is partly due to differences in resource distribution. Another source of variation could be the diverse census methods used (Mohr 1940; Johnson 1981). Researchers may count singing males, pairs of birds, or nests in assessing bird densities. These different methods might result in major distortions when data are pooled. Studies similar to mine have shown, however, that significant relationships can still be detected when using data pooled from various sources (Damuth 1981; Peters and Wassenberg 1983; Calder 1984).

Average adult body weights (grams) were taken from Terres (1980), Des Granges (1980), and Bock and Lynch (1970). If a range of body weights was given, the median was used. When different male and female weights were given, the average of these was taken. Less than 5% of the species were excluded because their body weights were not listed in any of the three sources. The birds were divided into carnivores, herbivores, or omnivores. Carnivorous birds were further subdivided into insectivores and raptors.

Regression analysis of density (D) against body weight (W) was performed on each data set using decimal logarithm transformations where $\log D = \log a + b \log W$.

RESULTS

The data for all the different sets are too numerous to list here. Although there was a wide scatter in the regressions (small R^2), 6 of the 29 regressions performed on the individual data sets were significant, with the R^2 values ranging from 0.20 to 0.49 and the slopes ranging from -0.21 to -1.12 . The consistently negative slopes of the regression lines and the fact that the six significant regressions are more than would be expected by chance alone (binomial distribution for individual terms; Parsons 1978) suggest that an inverse relationship between body size and density exists. Although only 18% of the variance was explained, the regression line was significant when all the data sets were pooled, suggesting a weak relationship (fig. 1). When the data were sorted by food type, the slopes of two of the three regressions did not differ significantly from zero (table 2). The carnivorous birds were the exception, but the significant regression explained only 27% of the variance. When raptorial birds were removed, the relationship remained significant, but only 9% of the variance was explained. When raptors alone were analyzed, the regression was still significant; the R^2 value was much higher and the slope was steeper than that for insectivorous birds.

DISCUSSION

The bird data covered a smaller range of body mass than the mammal data of Peters and Wassenberg (1983). This difference in range can affect R^2 values, but in no predetermined direction when using regression to analyze aggregations of subpopulations. Additionally, the lower R^2 obtained here is smaller than that expected solely from a reduction in the range of the independent variable (R. Lockhart, pers. comm.). The results for the raptors show that a smaller range can

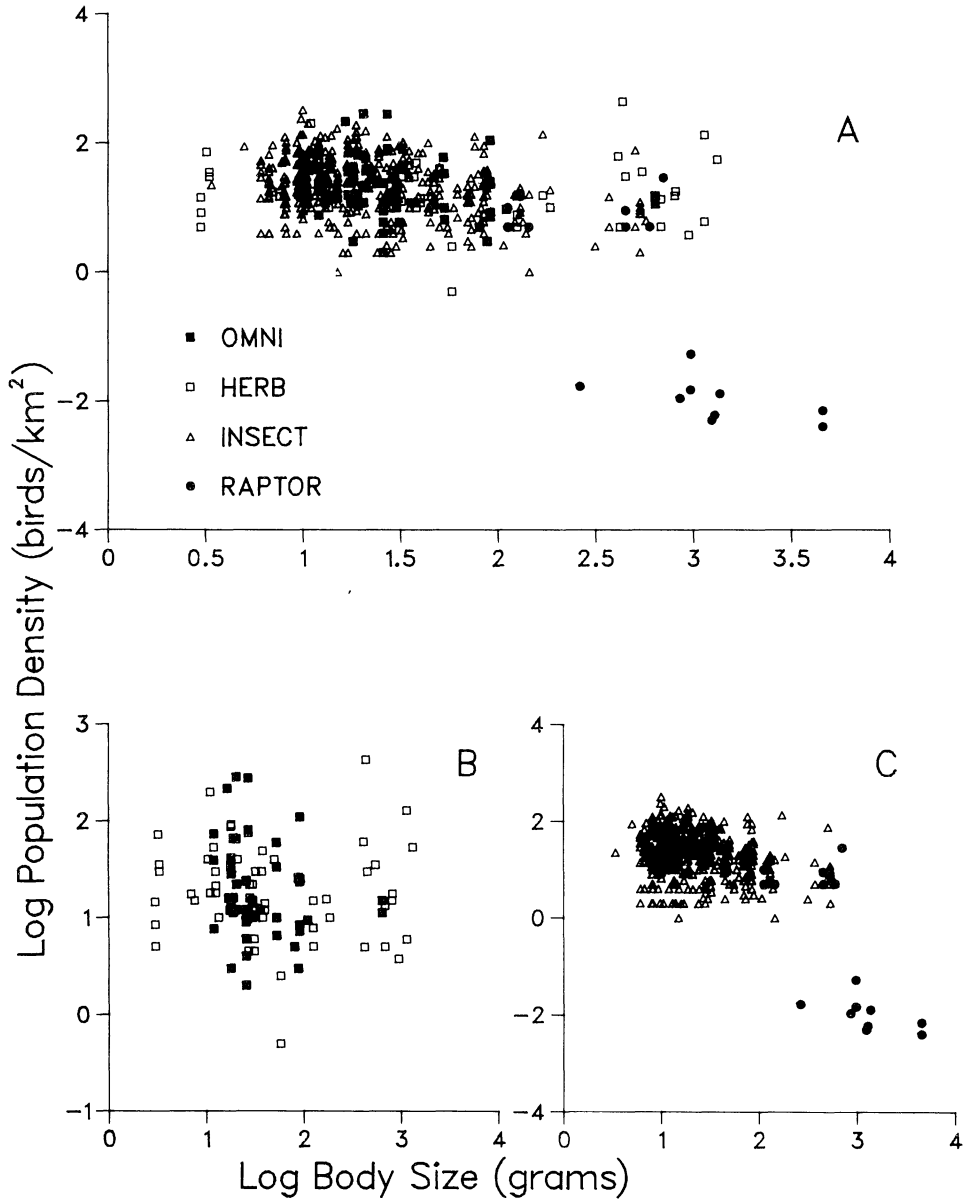


FIG. 1.—The relationship between body weight and population density. *A*, All data (omnivores, herbivores, insectivores, and raptors); *B*, omnivores and herbivores; *C*, carnivores (i.e., insectivores and raptors). For statistics describing each regression, see table 2.

TABLE 2

STATISTICS DESCRIBING REGRESSION OF LOG_{10} BODY SIZE (g) AGAINST LOG_{10} DENSITY (BIRDS/ km^2)

Group	Sample Size	y-Intercept	Slope	R^2	P	Ra	SE	LM
All data	564	1.96	-0.49	0.18	0.0001	3.0-4536.0	0.0436	1.2553
Carnivores	461	2.18	-0.67	0.27	0.0001	3.4-4536.0	0.0504	1.2528
Herbivores	56	1.29	-0.02	0.001	0.81	3.0-1320.5	0.0873	1.2578
Omnivores	47	1.63	-0.23	0.03	0.22	12.0-637.0	0.1819	1.2782
Insectivores	442	1.74	-0.31	0.09	0.0001	3.4-570.0	0.0470	1.3169
Raptors	19	5.57	-2.22	0.58	0.001	112.0-4536.0	0.4564	-0.4469

NOTE.—Body size is the independent variable; R^2 is the coefficient of determination; P is the probability that the slope is significant; Ra is the range of (linear) values of body size in grams; SE is the standard error of the regression coefficient; and LM is the mean of the dependent variable, log_{10} density.

TABLE 3

COMPARISONS OF ANIMAL DENSITIES AT THE MEAN BODY SIZE OF EACH GROUP (g) AS PREDICTED BY THE SPECIFIC RELATIONS FOR DENSITY AND BY THE GENERAL RELATION FOR ALL ANIMALS

	D1	D2	D1/D2	$\log(D1/D2)$
Animals (PW)	3.2×10^5	3.2×10^5	1	0
Mammals (PW)	210	85	2.5	0.39
Birds (PW)	11	550	0.020	-1.7
Carnivorous birds (PW)	9.2	700	0.013	-1.9
Birds	9.9	331.6	0.030	-1.5
Carnivorous birds	11.4	627.4	0.018	-1.7
Insectivorous birds	17.2	715.1	0.024	-1.61

NOTE.—D1 is the specific relation for density given in the number of animals per square kilometer. D2 is the population per square kilometer, where density = $10^{4.45} \times \text{weight}^{-0.98}$. PW refers to values obtained from Peters and Wassenberg (1983).

also give rise to a larger R^2 . Carnivorous mammals have a slightly wider size range than birds, yet show a highly significant relationship with a much larger R^2 (Peters and Raelson 1984). My data cover the natural range of avian body mass; thus, any poor scaling relationship could have an ecological rather than a statistical explanation.

Overall, the relationship between body size and density is weak but highly significant. This result, in comparison with Peters and Wassenberg's nonsignificant avian regressions, indicates the advantage of larger data surveys. The low correlation between the two variables for all nonraptorial birds (insectivorous, herbivorous, and omnivorous) suggests, however, that their densities cannot be accurately predicted from values of body weight. The comparison of animal densities at the mean body size of each animal group shows that the avian densities are between one and two magnitudes below the general curve for all animals but lie somewhat closer to this curve than in the Peters and Wassenberg study (table 3).

This result suggests that the general curve for all animals should not be used to predict densities of birds since only an approximation can be provided at best.

The results of my analyses indicate that raptors more than other birds show a stronger relationship between density and body size. This result supports the conclusions of Newton (1979), who used a larger sample and demonstrated that larger raptors breed at lower densities when compared to smaller raptors. His explanation was that larger raptors eat larger prey, which are less abundant. Damuth (1981) showed that density correlates strongly with body weight ($r = 0.86$) in mammals. Raptors may display a similar relationship simply because they must also adjust to the density of their mammalian prey. Furthermore, Schoener (1968) found a strong positive relationship between body size and range size in predatory birds and a weaker relationship for herbivores and omnivores. He proposed that this occurs because predators tend to feed on more exclusive areas and their food sources decrease with increasing predator weight. Herbivores and omnivores, however, show a higher occurrence of "gregarious nesting" (or no relationship) because of the greater patchiness of their food range.

The slopes for raptors are steeper than those for other carnivores, omnivores, and herbivores. This can be explained by reference to the rates of production of the potential prey populations relative to the demands of their predators. Larger predators eat larger prey (Schoener 1968); production per unit of mass declines with increasing size (Calder 1984), suggesting that larger prey supply less resource to larger predators per unit of time (Peters and Wassenberg 1983).

Other important variables that may affect the variation of bird densities are the quality and numbers of available nest sites (Newton 1979). A bird population can be very dense in one area if many possible nest locations exist. In other areas, with an equal amount of available food, the density will be much smaller if there are few appropriate nesting sites. Such an explanation may account for much of the variation obtained when performing regressions on the different data sets.

In conclusion, the relationship between body size and density in birds appears to be weaker than in mammals and other animals. Thus, any regression equation would provide only rough approximations of the real densities. The causes of this weakness cannot be explicitly identified in this study, although testable explanations of the patterns can be sought. One such explanation might be ecosystem structure. Mammals that are restricted to movement on land are also restricted to eating terrestrial prey. They essentially deal with two-dimensional habitats. Through flight, birds have available a great variety of food resources over a three-dimensional area, which could explain the poor correlation between body size and density. This hypothesis can be further tested by examining data for flightless birds.

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