

INDIVIDUALS–AREA RELATIONSHIPS: THE RELATIONSHIP BETWEEN ANIMAL POPULATION DENSITY AND AREA

EDWARD F. CONNOR,¹ AARON C. COURTNEY,² AND JAMES M. YODER³

¹*Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, California 94132 USA*

²*Perkins Coie LLP, 1211 SW Fifth Avenue, Suite 1500, Portland, Oregon 97204-3715 USA*

³*Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210 USA*

Abstract. We compiled studies that report data on the relationship between animal population density and patch or island area for 287 individual species and 21 faunas. We tested the assumption of the equilibrium theory of island biogeography that population densities are independent of area by performing a meta-analysis using the linear correlation coefficient, r , as a measure of the effect of area on population density. We fit meta-analyses that used a random-effects model to these data to test for the effects of taxa, habitat, latitude, spatial scale, and overall population density. We also fit meta-analyses that used a fixed-effect model to the same data to estimate the repeatability of measurements of the correlation between population density and area within species.

Contrary to the equilibrium theory of island biogeography, our results indicate that, on average, animal population densities are positively correlated with area, which suggests that density compensation may be uncommon. This result was found for individual species, but not for faunas. We found taxonomic differences in the correlation between population density and area, with insects and birds having on average large or moderately large positive correlations, respectively, and mammals having correlations near zero. Observations within individual species showed considerable repeatability. The observed overall positive correlation between the population density of individual animal species and area is best explained in the context of the resource concentration hypothesis.

Our results imply that the regional abundance and persistence of animal populations may depend strongly on the presence and continued persistence of a few large patches of suitable habitat, rather than on a regional network of small and large habitat patches.

Key words: *birds, population density; density compensation; equilibrium theory; insects, population density; island biogeography theory; mammals, population density; meta-analysis; population density; resource concentration.*

INTRODUCTION

The relationship between animal population density and area has been addressed explicitly by three ecological theories: the equilibrium theory of island biogeography (MacArthur and Wilson 1967), the phenomenon of density compensation (MacArthur et al. 1972), and the resource concentration hypothesis (Root 1973). While the theories of island biogeography and density compensation were initially motivated by studies of islands and the resource concentration hypothesis by studies of habitat patches, each of these theories has been interpreted and applied broadly to a variety of spatial scales and taxa (Janzen 1968, Simberloff 1974, Futuyma and Wasserman 1980, Faeth 1984, Dooley and Bowers 1996).

The equilibrium theory of island biogeography makes assumptions about population size, population density, and area in order to explain species–area relationships via the area per se hypothesis (MacArthur

and Wilson 1967, Simberloff 1976, Connor and McCoy 1979). The equilibrium theory of island biogeography assumes that the number of individuals within a taxon increases linearly with the area of an island (MacArthur and Wilson 1967:13). In other words, the theory presumes that population density remains constant with increasing area. While it is not explicit in their text, MacArthur and Wilson's (1967) assumption has been interpreted to apply to whole biotas, faunas, and communities, as well as to individual species (MacArthur and Wilson 1967, Simberloff 1988).

The implications of MacArthur and Wilson's (1967) assumption are quite different if they refer to groups of species (e.g., faunas) rather than to individual species. For individual species, their assumption implies that larger areas would contain more individuals of a species, but that the number per unit area would remain constant. However, since species richness (or group size) is a positive function of area, if we assume that the density of a group of species is constant for all areas, then the densities of individual species must, on average, decline in larger areas (Schoener 1986).

The phenomenon of density compensation attempts

Manuscript received 20 October 1997; revised 7 October 1998; accepted 5 January 1999; final version received 22 February 1999.

to account for observations that the summed density of animal species on small islands equals that of a mainland fauna (or of a fauna on larger islands), with the result that the average population density of each species is greater on smaller islands (MacArthur et al. 1972). This pattern is consistent with MacArthur and Wilson's (1967) assumption that density of animal groups is independent of area. Because there are fewer species on small islands, density compensation leads to the conclusion that, on average, island species have higher population densities than do mainland species. This pattern originally was interpreted to suggest that species on small islands were less subject to interspecific competition and predation, which allowed their populations to increase (MacArthur et al. 1972). However, Williamson (1981:240) and Schoener (1986) point out that if total faunal density is independent of island size (as assumed by MacArthur and Wilson 1967) and if a species-area relationship exists, we need not infer competitive release to account for density compensation. In any event, if density compensation is a widespread phenomena, we would expect that on average animal population densities should be inversely related to patch area.

The resource concentration hypothesis attempts to explain the often-observed phenomenon that habitat patches with large amounts of resources (e.g., monocultures, areas of high plant density, or large patches) have higher densities of insects (Root 1973, Kareiva 1983). Therefore, this hypothesis conjectures that population density should be positively correlated with patch area. The comparison of small and large habitat patches rather than homogeneous and heterogeneous habitat patches has provided a stronger test for the effect of resource concentration, since it is free from the confounding influences of habitat heterogeneity on food plant quality (Risch 1981, Kareiva 1983). Root (1973) conjectured that the higher density of animals in larger patches might be solely a consequence of movement behavior (the movement hypothesis); herbivores are more likely to find, and remain in, large, monospecific stands of their host plant than in small or heterogeneous patches. Other explanations include the enemies hypothesis, which suggests that predators are more effective in smaller patches than in large ones (Root 1973, Raupp and Denno 1979, Denno et al. 1981, Risch 1981, Kareiva 1983).

These three theories nearly exhaust the possibilities for the dependence of density on area. No theory has been proposed to suggest that areas of intermediate size should have higher or lower animal densities than should small and large areas.

We attempted to reconcile the theoretical expectations of equilibrium theory, density compensation, and resource concentration with empirical evidence concerning how the density of animal populations is related to area. A literature survey and meta-analysis of data on the relationships between animal population

density and patch area were used to determine whether the population densities of individual species and entire faunas, in general, are related to or independent of area. We considered mechanisms that may account for observed patterns in the relationship of population density and area for animals in different taxa, habitats, and latitudes, and at different spatial scales. Finally, we examined the implications of both theory and evidence concerning the relationships between animal population density and area in the context of biological conservation and the design of nature reserves.

METHODS

To determine whether the relationship between animal population density and area is consistent with the assumptions of the equilibrium theory of island biogeography or with the predictions of the resource concentration hypothesis, or if density compensation is common, we compiled data from the literature on animal population density in relation to area and examined these data via meta-analysis (Gurevitch et al. 1992, Gurevitch and Hedges 1993, Cooper and Hedges 1994, Arnquist and Wooster 1995).

Data compilation

Several methods were used to obtain data from as many studies as possible and to prevent bias in the selection of studies. We included studies of which we were aware initially and others suggested by colleagues. We also examined the literature cited in papers that reported data on animal population density in relation to area. Finally, we conducted a computer-assisted key word search of Biological Abstracts (BIOSIS) for the period 1978–1994. We used all combinations of the following groups of key words: (1) bird, mammal, insect, invertebrate, vertebrate; (2) density, abundance; (3) patch, plot, habitat; and (4) area, size.

All studies that reported data on the abundance or density of individual species in relation to a range of areas were included in our analysis. Only studies that reported areas and animal abundance or density in individual patches were used. For those papers in which the authors indicated they had collected data on animal abundance in relation to area, but had not published the data, we contacted the authors and attempted to obtain the data.

From our literature survey we located 34 different studies with data on the relationship between animal population density and area for 287 species. For 142 species, we obtained multiple estimates of the relationship between density and area from different studies. Most of the species for which we obtained data were birds (246 species from 14 studies), but data were also available on mammals (21 species from 11 studies) and insects (20 species from nine studies; Table 1). These studies included data on animal population density from a wide range of patch sizes and types, including some true island studies, but mostly comprised

TABLE 1. Relationship between population density of individual species and patch size.

Reference	Taxon	Number of species	Patch character	Patch size	Latitude (°)	CV	Sample size
Bach (1988)	insects	3	<i>Cucurbita maxima</i>	1, 4, 16, 36, 100, and 144 plants	42	148.41	36
Denno et al. (1981)	insects	6	<i>Spartina patens</i>	natural patches, <50–10 ⁵ m ²	40	...	15
Raupp and Denno (1979)	insects	10	<i>Spartina patens</i>	1, 3, 14, and 20 ha	39	95.16	4
Funderburke et al. (1990)	insects	1	<i>Glycine max</i>	rows of 3, 6, 12, and 24 m	31	61.32	24
Kindvall and Ahlén (1992)	insects	1	treeless heathland	natural patches, 0.25–64 ha	35	...	83
Cromartie (1975)	insects	3	<i>Brassica oleracea</i>	1, 10, and 100 plants	42	298.68	37
Karieva (1981)	insects	2	<i>Brassica oleracea</i>	1, 4, 8, and 16 plants	39	93.07	38–58
Maguire (1983)	insects	2	<i>Brassica oleracea</i>	9 and 81 plants	39	163.79	10
Matter (1997)	insects	1	<i>Asclepias syriaca</i>	natural patches, 1–96 plants	39	137.44	61
Gottfried (1979)	mammals	4	temperate forest	woodlots, 93–639 m ²	42	41.40	10
Geuse et al. (1985)	mammals	1	temperate forest	woodlots, 0.015–0.32 ha	50	11.11	20
Hanski and Kuitunen (1986)	mammals	5	coniferous forest	island, 0.3–8.0 ha	63	124.69	17
Laurance (1990)	mammals	5	tropical rainforest	fragments, 1.4–590 ha	15	229.98	10
Pahl et al. (1988)	mammals	5	tropical rainforest	fragments, 2.4–74.5 ha	17	98.29	11
Pokki (1981)	mammals	1	coniferous forest	islands, 0.29–1.0 ha	65	52.00	7
Foster and Gaines (1991)	mammals	3	successional field	32, 288, and 5000 m ²	39	314.90	55
Dooley (1993)	mammals	2	old field	patches, 0.0625–1 ha	39	95.50	12
Smith (1974)	mammals	1	rock	patches, 0.14–3.18 ha	34	119.30	25
Smith and Vrieze (1979)	mammals	3	hardwood forest	patches, 0.02–0.25 ha	26	113.61	6
Henderson et al. (1985)	mammals	1	deciduous forest	woodlots, 2.9–8.9 ha	45	41.35	5
Bond (1957)	birds	49	mixed forest	fragments, 6–202 ha	43	121.33	64
Haila et al. (1987)	birds	45	coniferous forest	fragments, 0.4–56 ha	61	167.48	34
Haila (1981)	birds	35	mixed forest	islands, 0.5–2680 ha	60	239.13	12
Haila et al. (1983)	birds	64	coniferous forest	islands, 0.5–582 ha	60	215.36	44
Haila (1983)	birds	41	coniferous forest	islands, 0.5–885 ha	69	208.74	41
Engbring et al. (1986)	birds	11	tropical rainforest	islands, 7, 85, 100, and 120 km ²	14	63.41	4
Askins et al. (1987)	birds	74	mixed forest	patches, 1–2633 ha	40	187.09	46
Blake and Karr (1987)	birds	53	deciduous forest	woodlots, 1.8–600 ha	40	224.05	15
Vickery et al. (1994)	birds	10	grassland	fragments, 0.3–404 ha	43	...	235
Willson et al. (1994)	birds	25	temperate rainforest	fragments, 0.5–350 ha	42	202.98	10
Møller (1987)	birds	32	rural farms	patches, 0.5–1.25 ha	57	147.62	70
Engbring and Ramsey (1989)	birds	14	tropical rainforest	islands, 4.81–141.97 km ²	14	134.42	4
Engbring et al. (1990)	birds	8	tropical rainforest	islands, 350, 109, 92, and 87 km ²	5	79.70	4
Rolstad and Wegge (1987)	birds	1	coniferous forest	woodlots, 0.45–1.55 km ²	60	...	12

Notes: Patch character and latitude are as listed by the original author; the mean latitude is listed if a range of latitudes was included in the original study. The coefficient of variation of the patch sizes, cv, was calculated by dividing the standard deviation of patch size by the mean patch size and multiplying by 100. Ellipses indicate that data were not available to permit calculation of cv.

data from natural and experimentally created habitat or crop patches. The Appendix contains a full description of the data for each individual species estimate and the data file used for the analysis.

Using the literature survey techniques described above, we also collected studies that reported data on the total population density of faunal groups rather than individual species. Thirteen of the 34 studies mentioned above included data on all species in a faunal group, so the density of the entire fauna could be calculated by summation. We located eight additional studies that reported only the density of the entire fauna in each area. These faunal studies consist of 16 avian, one mammalian, and four invertebrate data sets (Table 2).

Estimation of animal population density

The data sets we collected represent a heterogeneous group of field methods for estimating animal abundance or density. Most of the data on birds were obtained from point or transect counts during the breeding season, while mammalian abundance was estimated by mark, release, and recapture, and insect abundance by direct observation.

If animal densities in each area or patch studied were not directly reported, we calculated the density of individual species or faunas in each area from the abundance data reported. For avian studies using point counts (Bond 1957, Askins et al. 1987, Blake and Karr 1987, Vickery et al. 1994), we assumed that the detectability of a species was independent of patch size,

TABLE 2. Relationships between density of faunal groups and patch size.

Faunal group	Sample size	<i>r</i>	Latitude (°)	CV	Reference
Invertebrates					
Crustaceans	35	-0.49196	8	82.89	Abele and Patton (1976)
Spiders	5	0.77000	38	217.82	Mühlenberg et al. (1977)
Insects	9	-0.55226	10	120.87	Faeth and Kane (1978)
Insects	22	0.07670	53	283.75	MacGarvin (1982)
Vertebrates					
Mammals	17	0.23696	63	124.69	Hanski and Kuitunen (1986)
Avifauna	4	-0.93809	14	134.42	Engbring and Ramsey (1989)
Avifauna	4	-0.14570	14	63.41	Engbring et al. (1986)
Avifauna	46	-0.04220	40	187.09	Askins et al. (1987)
Avifauna	32	0.11863	32	61.16	Hamel et al. (1993)
Avifauna	41	-0.29655	69	208.74	Haila (1983)
Avifauna	30	0.51131	52	60.62	Woolhouse (1983)
Avifauna	10	-0.70977	44	104.70	Norment (1991)
Avifauna	16	-0.62779	51	83.73	Garay et al. (1991)
Avifauna	10	0.50918	42	202.98	Willson et al. (1994)
Avifauna	12	0.02503	60	239.13	Haila (1981)
Avifauna	34	-0.21898	61	198.71	Haila et al. (1987)
Avifauna	44	0.11684	60	215.36	Haila et al. (1983)
Avifauna	64	0.00940	43	121.33	Bond (1957)
Avifauna	15	0.35811	40	224.05	Blake and Karr (1987)
Avifauna	4	-0.04830	5	79.70	Engbring et al. (1990)
Avifauna	70	-0.23130	57	147.62	Møller (1987)

Notes: The *r* value is the linear correlation coefficient between the population density and patch area. Latitude is as given by the original author; the mean latitude is listed if a range of latitudes was included in the original study. CV was calculated as in Table 1.

and therefore we used the point count data as density estimates (Whitcomb et al. 1981, Lynch and Whigham 1984). Detectability of calling or singing birds will depend on stage of nesting, dominance hierarchies, vegetation, weather, and inter-observer variability, among other factors (Verner 1990, Blake 1992, Fancy 1997). However, if calling or singing rates are lower on small patches, then the results we obtained would reflect such patch-size-dependent behavior and not demographic differences between populations on small and large patches (McShea and Rappole 1997). For studies using transects to estimate avian abundance, we estimated densities by dividing the number of individuals observed by the area covered by the transect. In several instances, we contacted authors of studies to obtain further direction on how to estimate densities based on their data. In most of the mammal and insect studies, subsamples of the same size were taken within each area, and these values served as density estimates. Where unequal sampling effort was reported on different patches, we adjusted for differences in sampling effort in calculating density estimates.

We analyzed all estimates of density reported for a species, including those patches in which the abundance of a species was reported to be zero. Virtually all the data we report comes from studies of habitat patches, so unlike species-area studies or some studies of distribution-abundance correlations (Hanski et al. 1993), each species has had the opportunity to colonize every patch. In those few instances in which the authors reported that particular species had not had the opportunity to colonize every patch, we excluded those spe-

cies from the analyses (Engbring et al. 1986, 1989, Engbring and Ramsey 1990).

During the course of each study some species were not recorded on every patch. However, most studies consisted of a single field season, so the absence of a rare or less abundant species from some patches is to be expected, even though in some years (albeit infrequently) an individual or breeding pair may have been present (McArdle 1990). If we do not include these patches as zeros, then we will have thrown out data that says on average the densities in these patches approach zero. Strictly speaking, the density in patches where no individuals of a particular species were observed in the year of the study is not zero, but some small unobservable value, given the short duration of most studies. Were we to exclude these "zero" patches, we might be estimating the relationship between density and area for each species over a narrower range of areas. For a rare species that is usually found in large habitat patches, we might conclude that its density is independent of area, when in fact its probability of occurring on small patches, and therefore its density on small patches, is on average low or zero. It is counterintuitive to conduct an analysis that would permit such a biologically unreasonable conclusion. Because of sampling error it might even be possible for such a rare, forest-interior species to have a negative correlation between its density and patch area if only the currently occupied patches are included. Wright (1991) also argues that such "zero" patches should be included in studies of the correlation between distribution and abundance.

Statistical analysis of data

Meta-analysis is an extension of classical procedures for combining the results of independent statistical tests of the same null hypothesis to obtain a more general test of the common null hypothesis. Classical meta-analytic procedures combine probabilities (Becker 1994, Sokal and Rohlf 1995), but more recently developed meta-analyses are based on combining "effect sizes," a measure of the magnitude of the experimental effect (Rosenthal 1994, Shadish and Haddock 1994). Combining effect sizes is superior to combining probabilities because the same probability could be calculated from different studies if one study had a large sample size and a small effect size, and another had a large effect size and a small sample size (Becker 1994). However, effect sizes may be combined in an unambiguous way by weighting each effect size in proportion to its respective variance, which is in part a function of sample size (Shadish and Haddock 1994).

Estimation of effect sizes.—We selected the linear correlation coefficient, r , calculated from the correlation between animal population density and area, as our estimate of "effect size." For individual species estimates, the correlation coefficient between density and area was calculated for each individual species in each study. For faunal estimates, the correlation coefficient between the total density of the fauna and area was calculated in each study.

We use r as a descriptive measure of the degree of linear relationship between animal population density and area. When r is used in this manner, no assumption need be made concerning the marginal population distributions of the X and Y variates used in its computation (Cohen 1977). We chose r because procedures for the calculation and combination of effect sizes based on r are well developed (Hedges 1994, Raudenbush 1994, Rosenthal 1994, Shadish and Haddock 1994) and because most studies of the relationship between animal population density and area report r . Our use of the term "effect size" as a descriptor of r is not intended to imply that r is a measure of a causal relationship, but rather reflects the accepted usage in the literature on effect sizes and meta-analysis (Cohen 1977, Shadish and Haddock 1994).

The slope of the regression of density on area, the regression coefficient b_1 , might appear to be a useful measure of the effect of patch area on animal density, but no procedures for combining regression coefficients are available within the context of meta-analysis. To use b_1 the assumptions of regression, particularly that of variance homogeneity, must be satisfied for each species studied. We are unlikely to be able to do so using the same regression model for all species. Therefore, an omnibus model for all studies, like a log-log regression, would most likely involve using b_1 values from some portion of the studies where the fitted model is inadequate or displays significant lack-of-fit. If a

log-log transformation is used, the slope expected if densities are independent of area would be 1. The slope is then not a measure of the deviation of observation from expectation. In other words, the slope does not even measure the "effect" of the treatment area. We would have to use some statistic measuring the deviation of the observed from expected slope, perhaps from the d family of effect size metrics (Rosenthal 1994). Furthermore, in using the log-log transformation it is difficult to include patches where species are absent (zero patches), since the behavior of the $\log(n + 1)$ transformation will vary between species and its effect on b_1 is very unpredictable (although it depends on the number of zero patches and will always lead to a lower estimate of b_1 ; see Connor et al. 1997). Furthermore, in the bivariate case, the correlation coefficient equals the slope times a constant ($r = cb_1$, where $c = s_x/s_y$, and s_x and s_y = standard deviations of patch area and animal density, respectively; Draper and Smith 1981). Therefore, analyses based on r as a measure of the effect of patch area on animal density should describe the same pattern as would b_1 .

For studies that did not report r , or that did not provide the data necessary to calculate r , we used the procedures outlined in Rosenthal (1994) to estimate r from significance levels or other test statistics such as Student's t or F , in conjunction with the treatment means to determine the sign of r . To normalize the distribution of effect sizes, we used Fisher's transformation of r , Z_r , in our analyses (Rosenthal 1994, Sokal and Rohlf 1995).

We applied no transformations to the data from each study and did not include studies that only reported r values from transformed data. We did so because no tradition of a standard transformation for data relating animal density to patch area exists and because we wished to combine identical estimates of the effect of patch area on animal density from different studies.

Publication bias.—To determine whether a bias exists toward publishing only statistically significant correlations between animal population density and area, we plotted sample size against the absolute value of the effect size for individual species and faunas. If no publication bias exists, we would expect the average effect size to be independent of sample size. If a publication bias exists, the plot should be skewed, with few small values of the effect size estimate associated with small sample sizes (Begg 1994, Greenhouse and Iyengar 1994).

Combining effect sizes.—To examine the relationship between population density and area using individual species estimates, we combined effect size estimates among species and studies using the procedures outlined in Shadish and Haddock (1994), Hedges (1994), and Raudenbush (1994) for random-effects models. We fit random-effects models for all hypothesis tests because it is more appropriate to consider the effect size estimate for each species or fauna to be

drawn from an underlying distribution of effect sizes rather than to consider each species or fauna to be an estimate of a single common effect size. The random-effects meta-analysis is equivalent to a mixed-effects linear model, with the fixed effects as covariates and the random effects being the deviation of study i 's true effect size from the value predicted by the model (Raudenbush 1994). Similar procedures also were used to combine effect sizes for faunal studies. Weighted averages of effect sizes within various categories were obtained by weighting effect sizes by their variances. For random-effects models this consisted of weighting Z_r values by the reciprocal of the sum of their conditional variance ($1/(n - 3)$, where n is the sample size) and the random-effects variance (Raudenbush 1994). Random-effects variances were estimated using the iterative maximum likelihood procedure presented by Raudenbush (1994). Given that effect size estimates were weighted by their variances, model fitting involved weighted least-squares regression (Hedges 1994, Raudenbush 1994). Means and standard errors of effect sizes within groups were estimated, and mean Z_r values and their confidence limits were back transformed to units of r using the procedures outlined in Shadish and Haddock (1994).

When several species were observed within the same study, we treated each species as a separate, independent estimate of the relationship between animal population density and area. While it would be preferable to have each species' density-area relationship estimated in a different set of patches, restricting our analyses to such estimates would reduce our sample size tremendously. Furthermore, we see no a priori reason why assuming independence among species within a study should bias our results. Our treatment of multiple species within studies as independent estimates of the relationship between animal population density and area follows that used by Bowers and Matter (1997) and Bender et al. (1998).

Repeatability of effect size estimates.—We obtained multiple estimates of the correlation between population density and area for 142 of the 287 species. The majority of the species with multiple estimates were birds. To determine whether the effect sizes estimated for a species were repeatable, we examined the pattern of variation of effect sizes within species in two ways. First, we examined the tendency for species with multiple effect size estimates to have all of their effect size estimates of the same sign. A total of 374 effect size estimates were obtained for the 142 species that were examined in multiple studies. We conducted a randomization test to determine if the observed number of species homogeneous for the sign of effect size was statistically unusual, given independent assignment of negative and positive effect sizes among these 374 estimates. We placed the observed number of positive and negative effect sizes in a matrix constructed to mimic the number of effect sizes obtained for each

species (e.g., two, three, four, or five) and we counted the number of species homogeneous for sign of effect size with two, three, four, or five effect size estimates on each iteration. We performed 10 000 iterations and calculated the probability of obtaining the observed or a more extreme degree of homogeneity in the sign of effect size from the percentiles of the distribution of the results of the 10 000 iterations. Second, to test for repeatability in the magnitude of effect sizes within species, we fit a fixed-effect, one-factor model with study serving as factor levels and with repeated measures on species among studies to two subsets of the data. Estimates of effect sizes were obtained for 36 species of North American birds, (Bond 1957, Askins et al. 1987, Blake and Karr 1987) and for 14 species of Northern European birds (Haila 1981, Haila et al. 1983, 1987). These models allowed us to estimate the proportion of variation in the effect sizes of species shared between studies that is due to: (1) study-specific effects that would indicate a lack of repeatability, (2) differences between species, and (3) inherent observational variability (error). We report only study-specific effects since this is the only component of the variation in effect size that is related to repeatability.

Hypothesis tests.—To test the assumption of the equilibrium theory of island biogeography that animal population density is independent of patch area, we tested the hypothesis that the average effect size across individual species or faunas was significantly different from zero. The ratio of the overall mean effect size to its standard error is distributed as $N(0, 1)$, so if the ratio exceeds 1.96 or -1.96 , one would reject the null hypothesis at the $P = 0.05$ level (Shadish and Haddock 1994).

We computed the overall mean effect size for individual species and its standard error, as well as all models fit to test specific hypotheses about individual species using a single estimate of effect size for each species. We generated 100 data sets consisting of a single effect size estimate for each of the 287 species by including all species for which we had only a single estimate of effect size and by sampling at random within species for those species with multiple estimates. Summary statistics represent averages over the 100 data sets.

To determine if there were differences between taxa in average effect sizes, we fit a one-factor random-effects model to the effect size data using weighted least-squares regression ($n = 287$). A test of model significance is based on the model sums of squares, which is distributed as χ^2 with the respective model degrees of freedom (Raudenbush 1994). For mammals and birds only, we tested the hypothesis that average effect sizes were independent of habitat type by fitting a one-factor random-effects model ($n = 261$). For North American birds only, we tested the hypothesis that average effect sizes were unrelated to a species' habitat preference for forest interior, edge, or interior-

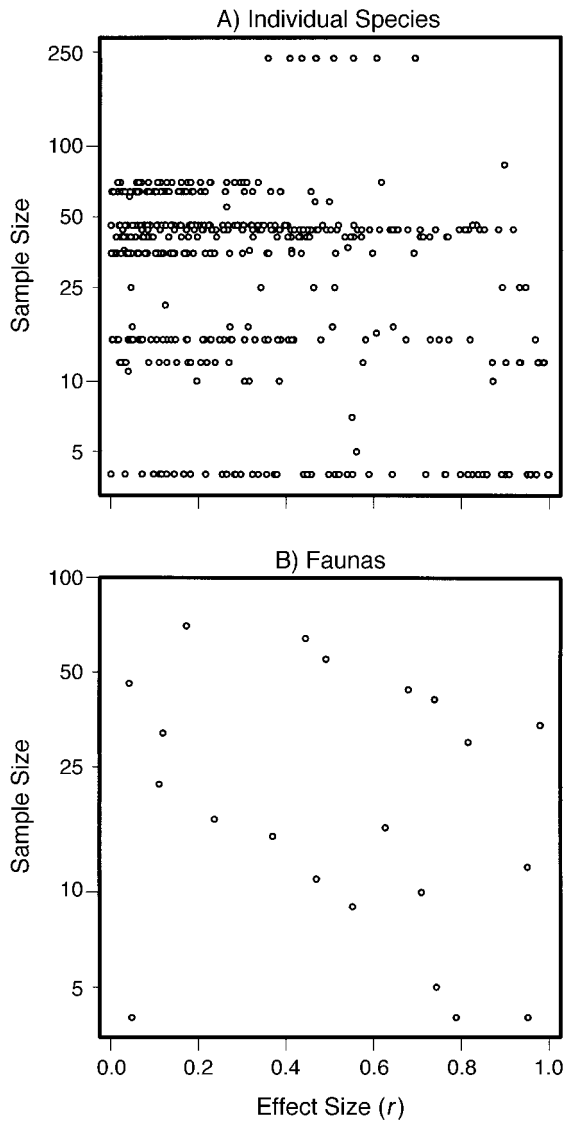


FIG. 1. Plots of the logarithm of sample size as a function of the absolute value of the effect size estimate, r , for (A) individual species ($n = 519$, which includes multiple estimates for some species) and (B) faunas ($n = 21$). The fact that small values of r are equally common regardless of sample size indicates that there is no bias against publishing small, statistically nonsignificant estimates of the correlation between animal population density and area for individual species. The absence of such values for faunas suggests that a bias exists against publishing nonsignificant values for faunas.

edge habitat by fitting a one-factor random-effects model ($n = 84$). Each species' habitat preference was classified according to schemes presented by Whitcomb et al. (1981) and Kendeigh (1982). Analyses were performed on each classification, but since the results were virtually identical we present only those based on the classification by Whitcomb et al. (1981).

To determine whether the effect size observed for a species was a function of the spatial scale at which a

study was conducted, we fit random-effects weighted least-squares regression models to data on the effect sizes for species for which the average size of patches included in the study could be expressed in hectares. Most insect studies report patch sizes as the number of plants and therefore were excluded from this analysis. Furthermore, because the average patch size for the studies by Engbring and Ramsey (1989) and Engbring et al. (1986, 1990) was two to three orders of magnitude greater than any other study, we analyzed the data with and without these studies included. To determine whether species whose average densities are low (e.g., rare species) tend to have positive or negative effect sizes, we fit a random-effects weighted least-squares regression model to the effect size data for species. Because the densities of mammals tend to be higher than those of birds, we fit the models separately to data on birds ($n = 240$) and mammals ($n = 19$). For the species for which density estimates for each patch and patch area could be expressed in hectares, we estimated an overall density for each species (λ_s) as

$$\lambda_s = \frac{\sum_{i=1}^n d_i a_i}{\sum_{i=1}^n a_i}$$

where d_i is the density of species s on patch i , and a_i is the area of patch i . Finally, to test if effect sizes are a function of latitude or the coefficient of variation in patch areas included in each study, we fit random-effects weighted least-squares regression models to the effect size data for all species or all faunas.

RESULTS

Individual species analyses

Publication bias.—The average effect size is independent of sample size for individual species, which indicates that no evidence for a bias against publishing small effect sizes is apparent in our data set (Fig. 1A).

Repeatability of effect size estimates.—A total of 374 effect size estimates were obtained for the 142 species that were examined in multiple studies. Of these estimates, 150 were negative and 224 were positive. A total of 64 of these 142 species were homogeneous for the sign of effect size (Table 3), and for all but species with five estimates the observed numbers homogeneous in sign of effect size were significantly greater than

TABLE 3. Summary of analysis of homogeneity in sign of effect size based on 10 000 iterations.

No. estimates per species	No. species	No. estimates homogeneous in sign	Expected no. estimates homogeneous in sign	
			Mean	SE
2	67	34	33.377	0.041
3	61	26	18.345	0.034
4	13	4	3.387	0.015
5	1	0	0.247	0.004

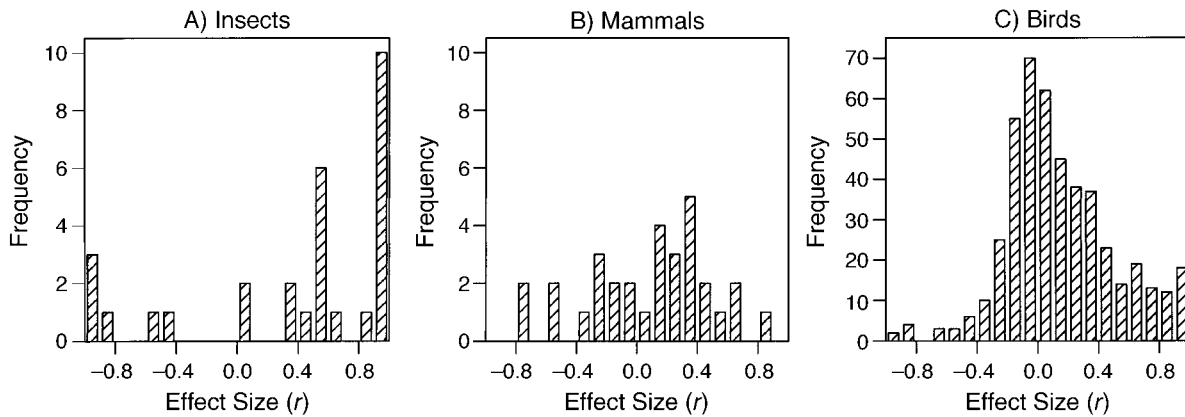


FIG. 2. Histograms of the magnitudes of the observed effect sizes, r , for (A) insects ($n = 29$), (B) mammals ($n = 31$), and (C) birds ($n = 459$). All values are reported, including values for species for which we obtained multiple estimates.

expected (greater than expected $+2$ SE). Furthermore, the pattern of the signs of the effect size estimates within species for which we had multiple estimates indicates that the probability of obtaining the observed degree of homogeneity in sign of effect size by chance alone is 0.0044. This suggests that at least the sign of the correlation between density and patch size may be viewed as a species attribute.

The fixed-effects, repeated-measures meta-analysis of the North American bird data indicated that 19% of the variation within species was due to differences among the studies, compared to only 13% for the Northern European bird data. The remaining variation within species was due to inherent observational variability, not to a lack of repeatability. While we have no standard against which to compare these values,

they suggest that the correlation between a species' density and patch area is largely an attribute of the species rather than of the study site and sampling methods.

Hypothesis tests.—Overall, the mean effect size for individual species ($r = 0.2233 \pm 0.0289$, mean ± 1 SE) was significantly greater than zero ($Z = 7.87$, $P < 0.0001$). This result is inconsistent with the assumption of the equilibrium theory of island biogeography that animal density is independent of island area. Effect size estimates for individual species were quite variable within all taxa (Fig. 2). The mean effect size for individual species, which did not differ significantly among taxa ($X^2 = 4.71$, $df = 2$, $P = 0.095$), was highest for insects and lowest for mammals (Fig. 3).

The mean effect sizes for birds and mammals did not differ significantly between habitat types ($X^2 = 2.03$, $df = 3$, $P = 0.566$), which may be due in part to high levels of variability in effect sizes in grassland and tropical forest habitats (Fig. 4). Among North American forest birds, species occupying forest-interior habitats had higher mean effect sizes than did those occupying interior-edge or forest-edge habitat ($X^2 = 14.97$, $df = 2$, $P = 0.0056$). The mean effect size of forest-edge species was negative (Fig. 5).

The spatial scale at which a study was conducted (measured as the average patch area) explained a significant amount of the variation in effect sizes when the studies by Engbring and Ramsey (1989) and Engbring et al. (1986, 1990) are included in the analysis ($X^2 = 5.27$, $df = 1$, $P = 0.0216$, $Z_r = 0.2206 + 0.00004[\text{average patch area}]$). However, when data from these studies are excluded from the analysis, the spatial scale of the study did not explain a significant amount of the variation in effect sizes ($X^2 = 3.63$, $df = 1$, $P = 0.0567$, $Z_r = 0.5776 + 0.00018[\text{average patch area}]$). The average density (λ_s) of each species did explain a significant amount of the variation in effect sizes for mammals ($X^2 = 5.073$, $df = 1$, $P = 0.0243$, $Z_r = 0.2606$

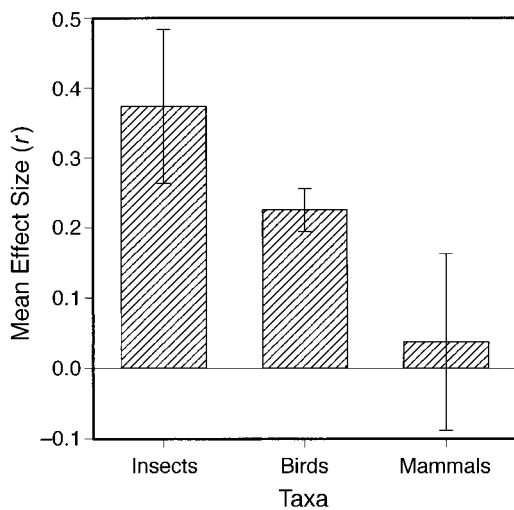


FIG. 3. Mean effect sizes (r) for individual species of insects, birds, and mammals. Vertical bars depict ± 1 SE. Results of a single-factor, random-effects model meta-analysis indicate significant differences in mean effect sizes among taxa.

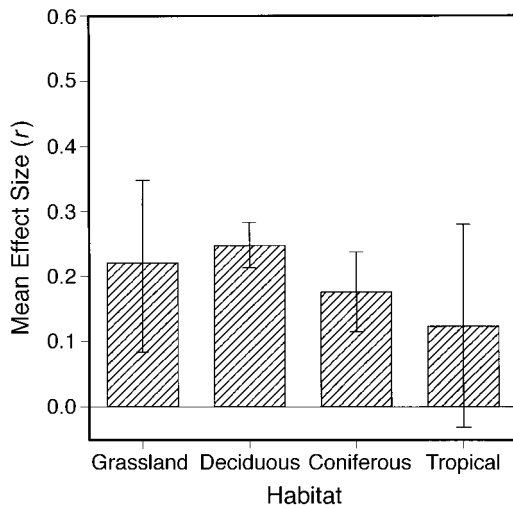


FIG. 4. Mean effect sizes (r) for individual species of birds and mammals in grassland and forest habitats. Vertical bars depict ± 1 SE. Results of a single-factor, random-effects model meta-analysis indicate no significant differences in mean effect sizes among habitats.

$-0.0081\lambda_s$), but not for birds ($X^2 = 1.294$, $df = 1$, $P = 0.2552$, $Z_r = 0.2328 - 0.0407\lambda_s$). Rare species were more likely to have higher effect sizes than common species. The latitude at which a species' effect size was estimated explained a significant amount of the variation in effect sizes ($X^2 = 5.81$, $df = 1$, $P = 0.016$, $Z_r = -0.0466 + 0.005556[\text{latitude}]$). The variability in patch size included within each study, as measured by the coefficient of variation in patch area, accounted for a significant component of the variation in effect size ($X^2 = 11.43$, $df = 1$, $P = 0.0007$, $Z_r = -0.1708 + 0.002075[\text{coefficient of variation in patch area}]$). Species whose effect sizes were estimated from a series of patches with a high coefficient of variation had larger effect sizes than did species whose effect sizes were estimated from a set of patches with less variability in area.

Faunal analyses

The low number of studies with small samples that report small r values suggests that a bias against publishing small effect sizes may be present in the set of faunal analyses included in our study (Fig. 1B). The overall mean effect size for faunas was negative, but not significantly different from zero ($r = -0.0711 \pm 0.0831$, $Z = -0.0712$, two-tailed $P > 0.94$). There was no difference in effect size between invertebrate and vertebrate faunas ($X^2 = 0.844$, $df = 1$, $P = 0.358$; Fig. 6). Neither the latitude at which a faunal study was conducted ($X^2 = 0.38$, $df = 1$, $P = 0.538$, $Z_r = -0.218 + 0.003[\text{latitude}]$) nor the coefficient of variation of the patch areas included in a faunal study explained a significant amount of the variation in the effect size ($X^2 = 0.898$, $df = 1$, $P = 0.343$, $Z_r = -0.26 + 0.00122[\text{coefficient of variation in patch area}]$).

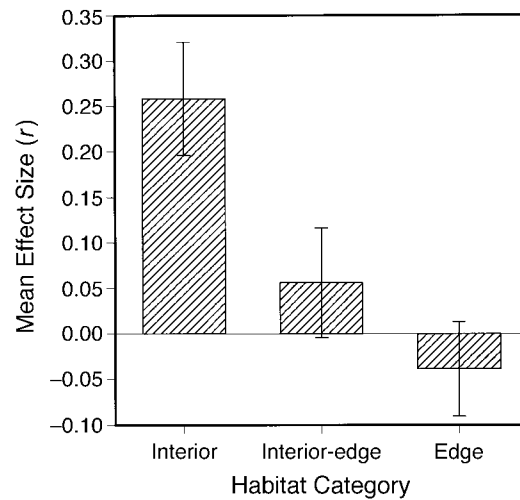


FIG. 5. Mean effect sizes (r) for individual species of North American birds that occupy forest-interior, interior-edge, or forest-edge habitats. Vertical bars depict ± 1 SE. Results of a single-factor, random-effects model meta-analysis indicate significant differences among species of birds occupying different habitats.

DISCUSSION

The overall positive correlation between population density and patch area that we observed for individual species is inconsistent with the assumption of the equilibrium theory of island biogeography that population density is independent of area. However, patch area, on average, accounts for approximately 5% of the variation in the population density of animal species, a moderate to small effect (Cohen 1977). Furthermore, the tendency for population densities of individual spe-

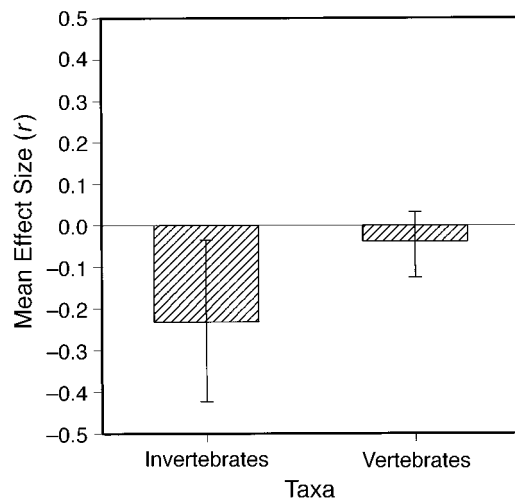


FIG. 6. Mean effect sizes (r) for vertebrate and invertebrate faunal groups. Vertical bars depict ± 1 SE. Results of a single-factor, random-effects model meta-analysis indicate no significant differences in the mean effect size between vertebrate and invertebrate faunal groups.

cies to be higher in larger rather than smaller areas suggests that density compensation is not a widespread phenomenon. On the other hand, the observation that individual species generally display higher population densities in larger areas is consistent with the resource concentration hypothesis. For whole faunas, the average correlation between density and area was slightly negative, but it was not significantly different from zero. While our sample size for faunas is low ($n = 21$), the evidence at hand is consistent with the equilibrium theory of island biogeography.

It is possible that our estimates of the correlation between animal population density and patch area are biased, but based on several lines of reasoning we argue that biased estimation of effect sizes is unlikely to account entirely for the patterns we observed. First, we contend that the methods we used to discover studies that report data on the relationship between population density and patch area are unbiased, and this is supported by the plot presented in Fig. 1A for individual species (Begg 1994, Greenhouse and Iyengar 1994). For faunas, the absence in the literature of studies with both small sample sizes and small effect sizes suggests that a bias exists against publishing statistically non-significant values of the correlation between faunal density and area. However, our selection of all studies, regardless of sample size, taxa, or the nature of the habitat patch, should be a sufficient guard against unforeseen bias on our part. Second, for studies of birds based on point counts, the radius of detection of many species may be greater than the radius of small patches. Therefore, the region sampled, a circle determined by the location of the sample point and a species' radius of detection, may not be entirely forested. As a result, there might be a tendency to underestimate densities on small patches, generating a positive bias in estimates of the correlation between bird population density and patch area (Haila 1988, Haila et al. 1993). While we have no means to quantify the extent of this problem, we note that even in studies such as Haila (1981, 1983) and Haila et al. (1983, 1987), in which density estimates are made using transects that cover the entire area of small patches, correlations between population density and patch area remain positive. Third, a large proportion of the effect size estimates we obtained were based on avian studies employing point count or transect methods that rely on detecting calling or singing birds. If there is a systematic bias for particular bird species, or bird species in general, to be more or less detectable as a function of patch area, then the patterns we report could simply reflect such a bias. However, the literature suggests that point and transect counts tend to underestimate abundance, not that the detectability of calling or singing birds depends on patch area (but see McShea and Rappole 1997). Fourth, Haila (1988) also suggests that because small patches contain more species that forage in regions outside the putative habitat patch than do large patches, density estimates

that do not account for this additional foraging area tend to be overestimates. Therefore, Haila (1988) claims that the null expectation for the relationship between density and patch area should be negative! Given that our estimates are on average positive, Haila's argument would imply that our effect sizes may be underestimates. Fifth, the repeatability of estimates within species in both the sign of the correlation and its magnitude suggests that the effect sizes that we have estimated are largely attributes of each species rather than idiosyncratic measures heavily dependent on site characteristics and study methodology. The high repeatabilities we observed also argue that it is unlikely that non-independence of species within studies could account for our results, since similar estimates of effect sizes were obtained regardless of the species composition of the fauna in which a species is imbedded. Finally, after excluding the studies by Engbring and Ramsey (1989) and Engbring et al. (1986, 1990) that have average patch areas at least two to three orders of magnitude greater than all other studies, we observed no effect of the spatial scale at which a study is performed on the correlation between population density and patch area for individual species. This result also supports our contention that the effect sizes we estimate are not systematically biased. In contrast, Bowers and Matter (1997) conclude that for mammals, density–area relationships are scale dependent, tending to be negative at small spatial scales. On the other hand, the coefficient of variation in patch area within a study was positively related to the correlation between population density and area, which indicates that variation in r is partly due to the idiosyncrasies of individual studies.

The overall positive correlation between population density and patch area could arise from a number of mechanistic explanations acting individually or in concert, and the mechanisms may differ among species. The enemies hypothesis and movement hypothesis have been suggested to underlie the resource concentration hypothesis (Root 1973, Risch 1981, Kareiva 1983) and could also explain the positive correlation between population density and patch area. Predation risk may be higher on small patches, keeping the densities of prey populations low (Smith 1974, Denno et al. 1981, Ambuel and Temple 1983, Askins et al. 1987, Rolstad and Wegge 1987, Møller 1991, 1995, Paton 1994), or animals may be less likely to disperse from large patches, keeping densities high (Raupp and Denno 1979, Foster and Gaines 1991). Habitat quality could be positively correlated with patch area, permitting higher density populations to persist (Ambuel and Temple 1983, Bach 1988, Møller 1991, 1995.). Social facilitation, higher probabilities of finding mates, or higher probabilities of over-winter survival or annual recolonization because of demographic or environmental stochasticity may lead populations in larger patches to avoid Allee or threshold effects, thus per-

sisting at higher mean densities than populations in small patches (Raupp and Denno 1979, Denno et al. 1981, Møller 1991, 1995). Andren (1994) found that positive correlations between density and patch area were more likely to occur in patch systems embedded in highly fragmented landscapes. While evidence is mounting that the movement hypothesis may explain the positive correlation between population density and patch area (Raupp and Denno 1979, Risch 1981, Karciva 1983, Foster and Gaines 1991), we believe that a better understanding of the mechanistic causes of the observed overall positive correlation between population density and patch area requires further field studies designed to test the potential role of these alternative mechanisms.

We observed substantial differences among taxa in the average correlation between population density and area for individual species, but not for faunas. For individual species, on average, insects and birds displayed large positive correlations, and mammals slightly positive correlations (Fig. 3). The average effect size for mammals is considerably less than that for birds and insects, and is not significantly different from zero. Our results parallel those reported by Bowers and Matter (1997) in their review of density–area relationships in mammals. Foster and Gaines (1991) suggest that at least for small mammals, greater numbers of individuals establish and hold territories on large patches, resulting in lower population densities on large than on small patches. Presumably, small mammal populations on small patches are composed of a greater proportion of transient or sub-adult individuals that are nonterritorial, hence permitting greater numbers of individuals to coexist temporarily on small patches (Dooley and Bowers 1996). Alternatively, mammals may have a greater tendency than insects and birds to use resources outside their putative habitat patches (Laurance 1990). Such resources would be more abundant and accessible near small patches because of their greater perimeter-to-area ratio (Bowers et al. 1996). However, since we report above that studies with larger coefficients of variation in patch area tend to have larger effect sizes, taxonomic differences in effect sizes also may be due in part to differences in the coefficient of variation in patch areas between taxa. Mammalian studies had smaller coefficients of variation in patch areas and smaller effect sizes than did birds or insects. All of these explanations could account for the low average effect size observed for mammals. For faunas, the sample size was low, particularly for insects and mammals (Fig. 6). Therefore, the lack of a difference between taxa among faunal studies may simply be an artifact of small sample size.

Our results do not appear to parallel those reported by Schoener (1986) for spiders and lizards on Bahamian islands. Schoener reported higher positive correlations between the abundance of several lizard species and island area than for several species of spiders. But,

when expressed as population densities (abundance divided by island area), rather than abundances, correlations for all species, both lizards and spiders, were negative. On the other hand, Diamond (1970) and Jaenike (1978) also found that the correlation between population density and patch area was positive, on average, for birds and insects. For both individual species and faunas more data are needed, particularly for insects, mammals, and other taxa besides birds, to represent accurately their respective correlations between population density and area.

Bender et al. (1998) performed a similar meta-analysis of the relationship between animal population density and patch area for species of birds, mammals, and insects. Their study focused on assessing the effect of habitat loss on population density at different spatial scales and in regions with differing proportions of suitable habitat. They report somewhat different effect sizes for each taxa, but we attribute these differences to their smaller data set ($n = 134$ species for Bender et al. 1998, and $n = 287$ species for our study). However, in most other respects their results are similar to those we report here.

Averaging across taxa for individual species, the correlation between population density and area is significantly greater among studies conducted in temperate and boreal environments than in tropical environments. We were able to include few tropical studies in our analyses (only four studies, consisting of 45 species), and these studies often used sampling methods that differed from the temperate and boreal studies we included. Therefore, we hesitate to propose any specific biological mechanism to account for this trend. For example, the studies by Engbring and Ramsey (1989) and Engbring et al. (1986, 1990) represent 93% of our tropical estimates of effect sizes for individual species and are based on the lowest sample size of the studies we include ($n = 4$ islands). These studies also sample bird species abundance by a hybrid method that combines point counts and transects, while most of the temperate and boreal studies of birds used point count *or* transect methods (Bond 1957, Haila 1981, 1983, Haila et al. 1983, 1987, Askins et al. 1987, Blake and Karr 1987, Møller 1987).

We observed no differences among broad habitat categories in the average correlation between population density and area for individual species of birds or mammals (Fig. 4). When we restricted our analyses to birds that occupy forest habitats, however, we found that bird species that occupy forest-interior habitats had higher correlations between population density and area than did species that occupy interior-edge or forest-edge habitats (Fig. 5). Bender et al. (1998) report similar results from their meta-analysis of avian density–area relationships. While this appears to be a striking result, we suggest that it may be simply a result of sampling methods combined with differences in the proportion of habitat that is classified as edge, interior-edge, or

forest interior on small vs. large patches. Forest-interior and interior-edge habitats constitute a larger proportion of habitat on large patches, and forest-edge habitat constitutes a smaller proportion of habitat on large patches. The change in the abundance of each habitat as a function of patch area, combined with the fact that point counts are usually conducted either in the center or at least some minimum distance from the forest edge, could result in a greater proportion of the habitat sampled on large patches being forest-interior habitat and a smaller proportion being forest-edge habitat, which in turn could lead to higher estimates of the density of forest-interior and lower estimates for forest-edge species on large patches. Alternatively, any of the mechanisms mentioned above could account for the higher densities of forest-interior and lower densities of forest-edge species in large patches. Finally, Stamps et al. (1987) also propose a mechanism to account for higher densities of forest-interior species on large patches based on an hypothesized relationship between patch area and intruder pressure.

Besides rejecting an assumption of the equilibrium theory of island biogeography, the overall positive correlation between the population density of individual species and patch area that we report has implications for the interpretation of species–area relationships, for the structure of metapopulation and patch dynamic models, and for the design of nature preserves.

Two of the mechanisms proposed to account for species–area relationships—the area per se hypothesis and the passive sampling hypothesis—require in the former case that the average total abundance of individual species populations be larger on large islands, and in the latter case that the number of colonists arriving is proportionately higher on large than on small islands (Connor and McCoy 1979). If the higher density of animals on large patches is due to local reproductive recruitment, then area per se leads to larger population sizes, thus lowering extinction rates and permitting more species to occupy large patches (Simberloff 1976, Connor et al. 1983). If the higher density of animals on large patches is generated by differential movement into large patches or higher movement rates out of small patches with equal rates of local reproductive recruitment in patches of all sizes, then the passive sampling hypothesis would account for the arrival and persistence of more species on large patches. Because movement may be more common among habitat islands than among true islands, we suggest that the area per se hypothesis combined with the habitat diversity hypothesis is more likely to explain species–area relationships on true islands (Connor and McCoy 1979), although this may not be the case for migratory birds that recolonize habitat patches annually (Haila et al. 1993).

The question of whether the dynamics of populations occurring on habitat islands are dominated by movement or by local reproductive recruitment, and hence

whether the passive sampling or the area per se hypothesis accounts for species–area relationships among habitat islands, is central to the concept of the metapopulation. Like equilibrium theory, most current models of metapopulation dynamics assume that population densities are independent of patch area (Hanski 1991, 1994, Hanski and Thomas 1994). Hence, while large patches contain larger populations than do small patches, their value per unit area to the regional abundance of a species is identical. Our result suggests, however, that on average population density is positively correlated with patch area. This implies that a few large patches may account for the regional abundance of a species, with small patches contributing little to regional abundance and persistence. If this is true, then recolonization dynamics may play a small role in the regional persistence of a species, and persistence would be insured by the preservation of a small number of large habitat patches containing large, extinction-resistant populations (Harrison 1991). Only when most habitat patches are too small to permit sufficient interannual *in situ* reproductive recruitment would the system be dominated by colonization and extinction dynamics.

Finally, if a goal of biological conservation is to maintain populations of individual species that are at least larger than some minimum viable population size, the observation that animal population densities are, on average, positively correlated with patch area argues that a single large nature preserve is more likely to achieve this goal than several small preserves of equal total area. For bird species, we observed the correlation between population density and patch area to be independent of the overall density of the species, which suggests that rare or uncommon species are as likely to have high positive correlations as are more abundant species. For mammals, rare species tend to have larger positive correlations between population density and patch area than do common species, which may even have negative correlations. Therefore, larger habitat patches are particularly valuable to rarer mammal species. However, the high variability in effect size estimates among species within taxa (Fig. 2), combined with the considerable repeatability in effect sizes we estimated within species, argues that the area dependence of the population density of individual species also varies considerably among species. As a result, the mean effect size within taxa will be an inadequate representation of the effect size for any particular species. Therefore, which conservation strategy is most effective will depend on the biology of the species in question, on the sign and magnitude of the correlation between its population density and area, and on many other biological and practical considerations.

ACKNOWLEDGMENTS

We would like to thank R. Askins, J. Blake, J. Dooley, Y. Haila, S. Matter, and A. Møller for providing unpublished data for our analysis. We would especially like to thank Y.

Haila for many stimulating suggestions pertaining to this work and S. Raudenbush for guidance through the meta-analysis maze. This manuscript benefited greatly from the thoughtful comments of M. Auerbach, R. Askins, J. Blake, B. Boecklen, M. Bowers, T. Case, J. Dooley, Y. Haila, S. Harrison, S. Matter, A. Møller, R. Osenberg, and D. Simberloff. This research was supported by NSF Grant BBS 91-12013.

LITERATURE CITED

- Abele, L. G., and W. K. Patton. 1976. The size of coral heads and the community biology of associated decapod crustaceans. *Journal of Biogeography* **3**:35-47.
- Ambuel, B. and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057-1068.
- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**:355-366.
- Arnquist, G., and D. Wooster. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution* **10**:236-240.
- Askins, R. A., M. J. Philbrick, and D. S. Sugeno. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* **39**:129-152.
- Bach, C. 1988. Effects of host plant patch size on herbivore density: patterns. *Ecology* **69**:1090-1102.
- Becker, B. J. 1994. Combining significance levels. Pages 215-230 in H. Cooper and L. V. Hedges, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Begg, C. B. 1994. Publication bias. Pages 399-409 in H. Cooper and L. V. Hedges, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79**:517-533.
- Blake, J. G. 1992. Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *Condor* **94**:265-275.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* **68**:1724-1734.
- Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. *Ecological Monographs* **27**:351-384.
- Bowers, M. A., K. Gregario, C. J. Brame, S. F. Matter, and J. L. Dooley. 1996. Use of space and habitats by meadow voles at the home range, patch and landscape scales. *Oecologia* **105**:107-115.
- Bowers, M. A., and S. F. Matter. 1997. Landscape ecology of mammals: relationships between density and patch-size. *Journal of Mammalogy* **78**:999-1013.
- Cohen, J. 1977. *Statistical power analysis for the behavioral sciences*. Academic Press, New York, New York, USA.
- Connor, E. F., S. H. Faeth, and D. Simberloff. 1983. Leafminers on oak: the role of immigration and in situ reproductive recruitment. *Ecology* **64**:191-204.
- Connor, E. F., E. Hosfield, D. Meeter, and X. Nui. 1997. Tests for aggregation and size-based sample-unit selection when sample units vary in size. *Ecology* **78**:1238-1249.
- Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. *American Naturalist* **113**:791-833.
- Cooper H., and L. V. Hedges, editors. 1994. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Cromartie, W. J., Jr. 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* **12**:517-533.
- Denno, R. F., M. J. Raup, and D. W. Tallamy. 1981. Organization of a guild of sap-feeding insects: equilibrium vs. nonequilibrium coexistence. Pages 151-181 in R. F. Denno and H. Dingle, editors. *Insect life history patterns: habitat and geographic variation*. Springer-Verlag, New York, New York, USA.
- Diamond, J. M. 1970. Ecological consequences of island colonization by South Pacific birds. Volume 2. The effect of species diversity on total population density. *Proceedings of the National Academy of Sciences, USA* **67**:1715-1721.
- Dooley, J. L. 1993. Patch effects on rodent demography. Dissertation. University of Virginia, Charlottesville, Virginia, USA.
- Dooley, J. L., and M. A. Bowers. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. *Oikos* **75**:543-562.
- Draper, N., and H. Smith. 1981. *Applied regression analysis*. Second Edition. John Wiley & Sons, New York, New York, USA.
- Engbring, J., and F. L. Ramsey. 1989. A 1986 survey of the forest birds of American Samoa. U.S. Fish and Wildlife Service, Department of the Interior, Washington, D.C., USA.
- Engbring, J., F. L. Ramsey, and V. J. Wildman. 1986. Micronesian forest bird survey, 1982: Saipan, Tinian, Agiguan, and Rota. U.S. Fish and Wildlife Service, Department of the Interior, Washington, D.C., USA.
- Engbring, J., F. L. Ramsey, and V. J. Wildman. 1990. Micronesian forest bird surveys, the Federated States: Pohnpei, Kosrae, Chuuk, and Yap. U.S. Fish and Wildlife Service, Department of the Interior, Washington, D.C., USA.
- Faeth, S. H. 1984. Density compensation in vertebrates and invertebrates: a review and an experiment. Pages 491-509 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Faeth, S. H. and T. C. Kane. 1978. Urban biogeography: city parks as islands for Diptera and Coleoptera. *Oecologia* **32**:127-133.
- Fancy, S. G. 1997. A new approach for analyzing bird densities from variable circular-plot counts. *Pacific Science* **51**:107-114.
- Foster, J., and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* **72**:1358-1373.
- Funderburke, J. E., A. R. Soffes, R. D. Barnett, D. C. Herzog, and K. Hinson. 1990. Plot size and shape in relation to soybean resistance for velvetbean caterpillar (Lepidoptera: Noctuidae). *Journal of Economic Entomology* **83**:2107-2110.
- Futuyma, D., and S. Wasserman. 1980. Resource concentration and herbivory in oak forests. *Science* **210**:920-922.
- Garay, G., W. E. Johnson, and W. L. Franklin. 1991. Relative abundance of aquatic birds and their use of wetlands in the Patagonia of southern Chile. *Revista Chilena de Historia Natural* **64**:127-137.
- Geuse, P., V. Bauchau, and E. Le Boulengé. 1985. Distribution and population dynamics of bank voles and wood mice in a patchy woodland habitat in central Belgium. *Acta Zoologica Fennica* **173**:65-68.
- Gottfried, B. M. 1979. Small mammal populations in woodlot islands. *American Midland Naturalist* **102**:105-112.
- Greenhouse, J. B., and S. Iyengar. 1994. Sensitivity analysis and diagnostics. Pages 383-398 in H. Cooper and L. V. Hedges, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: com-

- binning the results of independent experiments. Pages 378–398 in S. Schiener and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* **140**:539–572.
- Haila, Y. 1981. Winter bird communities in the Aland archipelago: an island biogeographic point of view. *Holarctic Ecology* **4**:174–183.
- Haila, Y. 1983. Colonization of islands in a north-boreal Finnish lake by land birds. *Annales Zoologici Fennici* **20**:179–197.
- Haila, Y. 1988. Calculating and miscalculating density: the role of habitat geometry. *Ornis Scandinavica* **19**:88–92.
- Haila, Y., I. K. Hanski, and S. Raivio. 1987. Breeding bird distribution in fragmented coniferous taiga in southern Finland. *Ornis Fennica* **64**:90–106.
- Haila, Y., I. K. Hanski, and S. Raivio. 1993. Turnover of breeding birds in small forest fragments: the “sampling” hypothesis corroborated. *Ecology* **74**:714–725.
- Haila, Y., O. Järvinen, and S. Kuusela. 1983. Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *Journal of Biogeography* **10**:499–531.
- Hamel, P. B., W. P. Smith, and J. W. Wahl. 1993. Wintering bird populations of fragmented forest habitat in the central basin, Tennessee. *Biological Conservation* **66**:107–115.
- Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models, and observations. *Biological Journal of the Linnean Society* **42**:17–38.
- Hanski, I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* **63**:151–162.
- Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pages 108–116 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.
- Hanski, I., and J. Kuitunen. 1986. Shrews on small islands: epigenetic variation elucidates population stability. *Holarctic Ecology* **9**:193–204.
- Hanski, I., and C. D. Thomas. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biological Conservation* **68**:167–180.
- Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society* **42**:73–88.
- Hedges, L. V. 1994. Fixed effects models. Pages 285–300 in H. Cooper and L. V. Hedges, editors. The handbook of research synthesis. Russell Sage Foundation, New York, New York, USA.
- Henderson, M. T., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. *Biological Conservation* **31**:95–105.
- Jaenike, J. 1978. Effect of island area on *Drosophila* population densities. *Oecologia* **36**:327–332.
- Janzen, D. H. 1968. Host plants as islands in evolutionary and contemporary time. *American Naturalist* **102**:592–595.
- Kareiva, P. M. 1981. Non-migratory movement and the distribution of herbivorous insects: experiments with plant spacing and the application of diffusion. Dissertation. Cornell University, Ithaca, New York, USA.
- Kareiva, P. M. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pages 259–289 in R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, New York, USA.
- Kendeigh, S. C. 1982. Bird populations in east-central Illinois: fluctuations, variations, and development over a half-century. *Illinois Biological Monographs* **52**.
- Kindvall, O., and I. Ahlén. 1992. Geometrical factors and metapopulation dynamics of the bush cricket, *Metrioptera bicolor philippi* (Orthoptera: Tettigoniidae). *Conservation Biology* **4**:520–529.
- Laurance, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy* **71**:641–653.
- Lynch, J. F., and D. F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* **28**:287–324.
- MacArthur, R. H., J. M. Diamond, and J. R. Karr. 1972. Density compensation in island faunas. *Ecology* **53**:330–342.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- MacGarvin, M. 1982. Species-area relationships of insects on host plants: herbivores on rosebay willowherb. *Journal of Animal Ecology* **51**:207–223.
- Maguire, L. 1983. Influence of collar patch size on population densities of Lepidopteran pests (Lepidoptera: Pieridae, Plutellidae). *Environmental Entomology* **12**:1415–1419.
- Matter, S. 1997. Population density and area: the role of between and within patch processes. *Oecologia* **110**:533–538.
- McArdle, B. H. 1990. When are rare species not there? *Oikos* **57**:276–277.
- McShea, W. J., and J. H. Rappole. 1997. Variable song rates in three species of passerines and implications for estimating bird populations. *Journal of Field Ornithology* **68**:367–375.
- Møller, A. P. 1987. Breeding birds in habitat patches: random distribution of species and individuals? *Journal of Biogeography* **14**:225–236.
- Møller, A. P. 1991. Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. *Ecology* **72**:1336–1349.
- Møller, A. P. 1995. Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. *Oikos* **72**:228–234.
- Mühlenberg, M., D. Leipold, H. J. Mader, and B. Steinhauer. 1977. Island ecology of arthropods. *Oecologia* **29**:117–134.
- Norment, C. 1991. Bird use of forest patches in the subalpine forest-alpine tundra ecotone of the Beartooth Mountains, Wyoming. *Northwest Science* **65**:1–9.
- Pahl, L. I., J. W. Winter, and G. Heinsohn. 1988. Variation in responses of arboreal marsupials to fragmentation of tropical rainforest in northeastern Australia. *Biological Conservation* **46**:71–82.
- Paton, P. W. C. 1994. The edge effect on avian nest success: How strong is the evidence? *Conservation Biology* **8**:17–26.
- Pokki, J. 1981. Distribution, demography and dispersal of the field vole, *Microtus agrestis*, in the Tvärminne archipelago, Finland. *Acta Zoologica Fennica* **164**:1–48.
- Raudenbush, S. W. 1994. Random effects models. Pages 301–322 in H. Cooper and L. V. Hedges, editors. The handbook of research synthesis. Russell Sage Foundation, New York, New York, USA.
- Raupp, M. J., and R. F. Denno. 1979. The influence of patch size on a guild of sap-feeding insects that inhabit salt marsh grass *Spartina patens*. *Environmental Entomology* **8**:412–417.
- Risch, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology* **62**:1325–1340.
- Rolstad, J., and P. Wegge. 1987. Distribution and size of

- capercaillie leks in relation to old forest fragmentation. *Oecologia* **72**:389–394.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecological Monographs* **45**:95–120.
- Rosenthal, R. 1994. Parametric measures of effect size. Pages 231–244 in H. Cooper and L. V. Hedges, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Schoener, T. W. 1986. Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? Pages 556–586 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- Shadish, W. R., and C. K. Haddock. 1994. Combining estimates of effect size. Pages 261–281 in H. Cooper and L. V. Hedges, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Simberloff, D. 1974. Equilibrium theory of island biogeography. *Annual Review of Ecology and Systematics* **5**:161–182.
- Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. *Ecology* **57**:629–648.
- Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**:473–511.
- Smith, A. T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. *Ecology* **55**:1112–1119.
- Smith, A. T., and J. M. Vrieze. 1979. Population structure of Everglades rodents: responses to a patchy environment. *Journal of Mammalogy* **60**:778–794.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third edition. W. H. Freeman, New York, New York, USA.
- Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. *American Zoologist* **27**:307–325.
- Verner, J. 1990. Analyst and observer variability in density estimates from spot mapping. *Condor* **92**:313–325.
- Vickery, P. D., M. L. Hunter, Jr., and S. M. Melvin. 1994. Effects of habitat area on the distribution of grassland birds in Maine. *Conservation Biology* **8**:1087–1097.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125–206 in R. L. Burgess and B. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Williamson, M. 1981. *Island populations*. Oxford University Press, Oxford, UK.
- Willson, M. F., T. I. De Santo, C. Sabag, and J. J. Armesto. 1994. Avian communities of fragmented south-temperate rainforests in Chile. *Conservation Biology* **8**:508–520.
- Woolhouse, M. E. J. 1983. The theory and practice of the species-area effect, applied to the breeding birds of British woods. *Biological Conservation* **27**:315–332.
- Wright, D. H. 1991. Correlations between incidence and abundance are expected by chance. *Journal of Biogeography* **18**:463–466.

APPENDIX

A full description of the data for each individual species estimate (summarized in Table 1) and the data file used for the analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E081–008. The data are posted both in tabular form and as a downloadable data set with accompanying metadata.