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Study design and interpretation of shrew (*Sorex*) density estimates

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Population density estimates are a significant aspect of ecological theory. Of the approximately 6000 shrew literature citations, we located none that compared shrew density estimates and explained their variation. We compared 476 usable estimates of shrew density reported in 27 publications for 10 of the 70 species in the genus *Sorex*. Several factors explained the variation in density, including study area size, year of study, site selection, sampling method, trap type, reported vegetation details, elevation, and body mass. Unlike many larger mammals, shrew numbers were often estimated at study areas too small to encompass "populations". The 59 study areas ranged in size from 0.041 to 9.975 ha, numerical estimates ranged from 0 to 249 shrews, and density estimates ranged from 0 to 17 667 shrews km^{-2}. The average numerical estimate was only 14 shrews and the highest densities were recorded at the smallest study areas. The numerical estimates and study area sizes of shrews were disproportionately small compared to estimates of highly carnivorous species of Carnivora. Our results can provide guidance for setting and designing future studies of shrew numerical patterns that could contribute substantially to knowledge of shrew biology.

Introduction

Considering that many ecological calculations utilize density estimates, the importance of their reliability cannot be overstated (Smith *et al.* 1971). The first step to improve the reliability and interpretability of density estimates is to explain as much of their variation as possible, and to identify the influences of study attributes on density estimates (Barbehenn 1974). Smallwood and Schonewald (1998) took this step for species of mammalian Carnivora, but to date, no such effort has been made for species of *Sorex*.

However challenging identifying the sources of variability in population size, the level of variation found has significant implications in the design and interpretation of ecological studies (Cyr 1997). Comparative studies on published density estimates were conducted for species of mammalian Carnivora (Smallwood & Schonewald 1998), pocket gophers (Smallwood & Morrison 1999), Swainson's hawk (Smallwood 1995), and northern goshawk (Smallwood 1999a). Such comparisons can help identify research needs, uncover recurring patterns in methodology and interpretation, and sources of variability.

Shrew population density estimates exhibit high variation. Densities were reported to range from 1 to 22.7 ha^{-1} for *Sorex cinereus* (Buckner 1966), 7.5 to 62.7 ha^{-1} for *S. arcticus* (Holling 1959), and 15.6 to 62.5 ha^{-1} for *S. fumerus* (Hamilton 1940). Several factors have been found or suspected to contribute to variation in shrew numbers, such as season (Churchfield 1980), elevation (Butterfield *et al*. 1981), habitat (Lee 1995), and whether the estimate is crude or ecological (Mohr 1943). In addition to high variation, Sheftel (1989) found a shrew population in central Siberia to be cyclic. There exist many more variables that can potentially contribute to variation in shrew population density, however a search through Haberl's (1995) comprehensive database did not produce a study of shrews that compared density estimates and tried to explain the variation introduced by study design attributes.

The goal of the present study was to explain the variation in reported shrew density estimates due to study and interpretive design attributes, such as study area size, trapping technique, season, and year of study. We also compared shrew densities with those of highly carnivorous species of mammalian Carnivora, because they occupy the same trophic level and their analysis has been completed (Smallwood & Schonewald 1998). We hope that these comparisons can serve as a status summary, or as a guide in designing future studies. When discussing the relationship between density and habitat, Van Horne (1983) suggested that thorough demographic investigations of one species across several habitats were needed to interpret broader studies. Perhaps these suggestions combined with our results can assist in generating more interpretable and reliable shrew density estimates.

Methods

Shrew density estimates were obtained from the literature through 1998. Although each potential publication was inspected for multiple variables (Table 1), the author(s) only had to state the study area size and their methods for the estimate to be included in the analysis. The variables measured from each report were those described in Smallwood and Schonewald (1998), and included the purpose of the study, site attributes, when the study was done, and methodological, interpretive, and reporting attributes. Additional variables to Smallwood and Schonewald (1998) were trap type (live trap, pitfall trap, snap trap), month of the estimate, and some of the estimators were different. These variables were summarized statistically as a means to describe studies conducted to estimate shrew density. This descriptive analysis was performed for all shrew density estimates, as well as for the estimates pooled into unique combinations of study, site, and species.

Most of the variables were then examined to estimate their relative magnitudes of effect on shrew density. We used graphing and linear regression analysis to examine the relationship of density with each of the other measured variables. Graphing and correlation matrices were used to detect high correlation between variables so that we could minimize multicollinearity when performing multiple regressions. We entered many combinations of variables into stepwise multiple regression analysis, selecting those that were more orthogonal to each other. Our objective was to find the most efficient models, or those that explained substantial variation in density with small sets of orthogonal variables. We developed these models for two sets of data, with and without estimates of 0 shrews km^{-2}. For regressions involving 0 shrews km^{-2}, we added 1 to all numerical estimates prior to transformation to density, thereby avoiding omissions of estimates when log transforming them.

Next, we compared shrew density estimates with the density estimates of highly carnivorous species of the mammalian order Carnivora, including *Alopex lagopus*, *Canis latrans*, *Canis*

Table 1. Summary of *Sorex* study attributes associated with density estimates, where *N* = number of estimates, ha = study area size in hectares (rounded to one decimal place), mark = mark-recapture, and capture = capture-recapture.

Species and source	Location	*N*	ha	Sampling	Vegetation
Sorex alpinus					
Nosek *et al*. 1972	Jivova, Czechoslovakia	1	0.9	mark	spruce forest clearing
Sorex araneus					
Buckner 1969	Berkshire, England	15	2	mark	oak glade
Churchfield *et al*. 1995	Berkshire, England	33	0.3	capture	grasslands, different succession
Dickman & Doncaster 1987	Oxford, England	5	0.3	live trap	long grass and shrub
Dickman 1980	Machynllenth, Wales	1	0.9	mark	mixed forest plantation
Hanski 1986	Finland	3	0.7–3.8	guess	none provided
Hansson 1968	Southern Sweden	37	0.6–3.8	removal	perennial grassland and hay field
Ivanter *et al*. 1994	Karelia, Russia	13	1–2	mark	spruce, birch forest
Kollars 1995	Munich, Germany	9	0.9–1.0	mark	spruce plantation
Moraleva & Telitzina 1994	Siberian plain, Russia	6	2.2–3.9	mark	mixed forest
Nosek *et al*. 1972	Jivova, Czechoslovakia	1	0.9	mark	spruce forest clearing
Pernetta 1976	Wytham, England	4	1.2	kill	grassland
Pernetta 1977	Wytham, England	26	0.8	mark	deciduous woodland
Pucek 1969	Northwestern Poland	15	5.8	removal	bog and woodland
Yalden 1974	Woodchester Park, France	2	0.4–1.8	mark	rough grassland
Yalden *et al*. 1973	Cap Gris Nez, France	1	0.3	capture	woodland, stone walls, grassland
Zukal 1993	Brno-City, Czechoslovakia	2	0.2	kill	oak-hornbeam forests
Sorex arcticus					
Buckner 1957	Winnipeg, Manitoba	29	2	capture	tamarack bog
Sorex caecutiens					
Hanski 1986	Finland	1	0.8	guess	none provided
Sorex cinereus					
Buckner 1957	Winnipeg, Manitoba	78	2	capture	tamarack bog
Cawthorn 1994	Westmoreland, Pennsylvania	2	1	mark	2° deciduous forest
Grodzinski 1971	Fairbanks, Alaska	4	1	capture	white spruce stand
Manville 1949	Huron Mountains, Michigan	28	2	trapping	woodland
Townsend 1935	Syracuse, New York	2	0.04	capture	swamp, mixed woodland
Sorex fumeus					
Cawthorn 1994	Westmoreland, Pennsylvania	1	1	mark	2° deciduous forest
Sorex hoyi					
Manville 1949	Huron Mountains, Michigan	2	0.8–1.9	trapping	sugar-maple-yellow birch
Sorex longirostris					
French 1980	Chambers Co., Alabama	2	0.1–0.4	trapping	hardwood forest
Smith *et al*. 1971		1	5.1	kill	lowland mesic-hardwood forest
Sorex minutus					
Ellenbroek 1980	Netherlands and near Ireland	20	0.5	mark	shrub, grass, spruce, deciduous woodland
Kollars 1995	Munich, Germany	9	1	mark	spruce plantation
Nosek *et al*. 1972	Jivova, Czechoslovakia	1	0.9	mark	spruce forest clearing
Pernetta 1976	Oxford University Estate	4	1	kill	grassland
Pernetta 1977	Wytham, England	26	0.8	mark	mixed deciduous woodland
Pucek 1969	Wytham, England	10	5.8	removal	bog and woodland
Zukal 1993	Northwestern Poland	1	0.3	kill	oak-hornbeam forests
Sorex vagrans					
Ingles 1961	Huntington Lake, California	1	0.5	mark	mixed fir, meadow, riparian
Newman 1976	Whatcom Co, Washington	13	1.3–1.8	mark	old field & woodland
O'Farrell & Clark 1986	Whirlwind Valley, Nevada	3	10	mark	marsh-meadow[1]

[1] Other habitats were trapped, but only marsh-meadow produced shrews

lupus, *Lycaon pictus*, *Vulpes velox*, *Acinonyx jubatus*, *Lynx canadensis*, *Lynx lynx*, *Lynx rufus*, *Puma concolor*, *Panthera leo*, *Panthera pardus*, *Panthera tigris*, *Herpestes javanicus*, *Crocuta crocuta*, *Lontra canadensis*, *Lutra lutra*, *Martes martes*, *Martes pennanti*, *Mustela erminea*, *Mustela frenata*, *Mustela nivalis*, *Mustela vison*, *Taxidea taxus*, and *Ursus maritimus*. These species, having already been analyzed (Smallwood & Schonewald 1998), can serve as a useful comparison group with which to interpret the variation in shrew density. For both taxonomic groups, we also compared their densities relative to their corresponding study area sizes and to the body masses typical of each species. We compared observed study area sizes of shrews to those predicted by the model of Carnivore study area size regressed on body mass, and we com-

Table 2. Statistical summaries of variables measured from reports of shrew density estimates in the literature.

Variable	Description: Frequency of estimates or range and mean values
Species	1 *Sorex alpinus*, 174 *S. araneus*, 79 *S. arcticus*, 29 *S. vagrans*, 3 *S. longirostris*, 1 *S. caecutiens*, 114 *S. cinereus*, 2 *S. hoyi*, 2 *S. fumeus*, 71 *S. minutus*
Study purpose	100% non-ideological, all for ecological or population research
Continent	48% North America, 52% Europe and western Asia,
Latitude	range 33°S to 65°N, mean = 50°N
Site selection	61% random, 32% based on prior knowledge of shrew presence, 7% unreported
Level of isolation	72% continental, 27% fragmented patch on mainland, 1% islands
Land use	63% unreported, 3% reserves, 3% game refuge, 3% multiple-use, 5% farmland, 1% urban, 21% University/government research land
Vegetation detail	4% unreported, 4% generic biomes, 23% type of biome, 65% dominant plant species, 4% detailed species composition
Vegetation categories	12% reported none, 25% described one Kuchler category, 52% gave 2–3, 11% gave 4–7
Dominant vegetation	20% grassland; 2% sage scrub; 24% deciduous, 5% broadleaf, 48% evergreen forest
Physical relief	3% mountains, 11% foothills, 3% rolling, 81% flat, 2% unreported
Elevation	range 0 to 2134 m above sea level, mean = 321 ± 322 m
Study area size	range 0.00041 to 0.09975 km^2, mean = 0.02 km^2.
Type of density	100% crude, mostly involving study "plots" or trap grids
Year of study	spanned 57 years from 1934 to 1990
Season	3% January, 2% February, 3% March, 3% April, 10% May, 12% June, 17% July, 12% August, 11% September, 10% October, 7% November, 3% December, 2% spring, 3% summer
Study duration	range 3 days to 4 years, mean 249 days
Type of trap	42% live, 19% pitfall, 8% snap, 30% combination, 0.8% unreported
Sampling	1% remote, 8% handling, 75% intensive handling, 16% kill-removal
Estimation intensity	5% guess, 16% census, 40% simple equations, 39% 0-capture models, 0% variance exhaustion
Comparison	26% not compared, 74% compared intra-specifically, none extrapolated to larger areas
No. of species	24% single-species, 31% 2–3 species, 45% ≥ 4 (maximum = 19)
Site map detail	37% no description, 37% text only, 5% location, 11% boundary, 5% topography or vegetation, 4% animal distribution
Status	100% made no mention of population status
Reliability of estimate	63% unreported, 11% "minimum" or "conservative", 9% over-estimates or representative of peak condition, 7% "accurate"
No. of captures	11.6% of the estimates, involved 2 to 320 animals and a mean of 75
Publication outlet	11% books, 4% wildlife management journals, 41% zoology/behavior journals, 37% ecology journals, 7% natural history journals

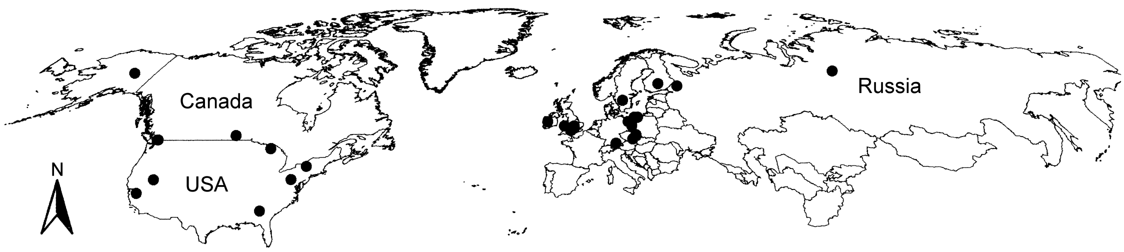

Fig. 1. The sites (circles) where *Sorex* density estimates were made.

pared observed shrew densities to those predicted by the model of Carnivore density regressed on study area size.

Estimates of shrew female body mass were collected from Jackson (1928), Pearson (1947), Rudd (1955), Hawkins and Jewell (1962), Buckner (1964), Churchfield *et al*. (1977), Churchfield (1981), Hanski (1984, 1989), Damuth (1987), and Innes (1994). Estimates of body mass among species of Carnivora were taken from sources referenced in Smallwood and Schonewald (1998).

Results

Study attributes

We collected 476 estimates of shrew density, but only 81 of these were unique combinations of study, site and species. We found estimates for 10 species of *Sorex* reported in 27 published reports, representing 14% of the recognized species of *Sorex* worldwide (Table 2). These estimates were made at only 25 sites, which were somewhat clustered in Europe and circumvented much of the North American interior (Fig. 1). Shrew density studies spanned over a 57 year period from 1934 to 1990, most frequently during the 1950s and 1960s. During this time, the most mathematically rigorous estimates, such as 0-capture estimators, were most common during the 1950s, whereas more simplistic estimators, such as census, direct recovery, and guessing, appear to be growing more frequent recently.

Compared with reports of Carnivore density, reports of shrew density tended to include more written detail of the vegetation on the study site and more of them represented month of the year rather than season, year, or a string of years (Table 2). However, maps of the study site were still too rare, especially those depicting vegetation and physical relief (Table 2). Also, shrew density was estimated only for the purpose of ecological or population study, rather than for conservation or management, as was so common for estimates of Carnivora. Fewer of the studies were from sites selected based on prior knowledge of the species' presence, or were dedicated to a single species. Fewer of the shrew studies lasted longer than a year, the majority employed intensive handling methods, but none reported accidental losses of study individuals due to trapping or handling. None of the density estimates were "ecological", none were extrapolated to larger areas, and surprisingly few were accompanied by descriptions of the land use on or around the study site. More were based on removal methods and more were compared intra-specifically to other estimates. None of the shrew density estimates were accompanied by an investigator's opinion of the condition or status of the population prior to, during, or following the study. Few were accompanied by an assessment of the reliability of the estimate.

Of the 81 unique combinations of study, site, and species, 27% were focused on a single species, 27% included estimates of 2 species, 22% included estimates of 3 to 8 species, and 24% included estimates of more species. Four estimates were made on islands, and the rest were made on mainland areas with 22 reporting some sort of physical barrier to dispersal nearby, such as ocean, lake, or urban areas. Only 15 sites were reportedly used for livestock grazing, hunting, or timber harvest. The terrain was flat at 67% of these sites, rolling at 18%, and mountainous at only 5.6%. The sampling meth-

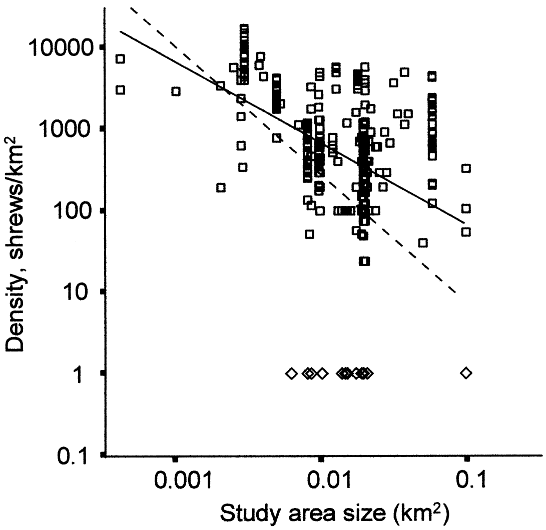

Fig. 2. Log density of shrews regressed on log study area size with (dashed line and all symbols) and without (solid line and squares) estimates of 0 shrews on the study site.

ods involved handling at 26% of these sites, intensive handling at 46%, and removal at 24%. The land use was not described for 59% of these sites, and it was urban at 6%, university and other special purpose government land at 16%, and multiple use at 6%.

Density

The average numerical estimate was 14 shrews (range 0 to 249) on an average study area size of 2 ha (range 0.041 to 9.975 ha). The average density was 1344 shrews km^{-2}, ranging from 0 to 17 667 shrews km^{-2} (Fig. 2). The shrews' typical or reported female body mass averaged 6.09 g (range 2.9 to 9.1 g). Contrary to most other taxonomic groups examined previously (e.g., Damuth 1987, Smallwood *et al.* 1996, Smallwood & Morrison 1999), log density increased nearly proportionally with increasing

Table 3. Unstandardized (b) and standardized (β) slope coefficients estimated for predictor variables of log density, using linear least squares regression (R^2 = 0.49, Root MSE = 0.52, df = 4, 371), and excluding all estimates of 0 shrews km^{-2}. (The unstandardized slope coefficient is useful for model prediction of density, and the standardized slope coefficient informs of the variable's relative contribution to the total sum of squares explained by the model.)

Predictor variable	Regression coefficients			
	a	b	SE of a, b	β
Intercept	1.454	–	0.535	–
Year of estimate	–	0.022	0.003	0.410
log Study area size (km^2)	–	–0.664	0.087	–0.336
log Female body mass (kg)	–	0.743	0.203	0.158
Number of vegetation categories reported	–	0.072	0.020	0.146

Table 4. Unstandardized (b) and standardized (β) slope coefficients estimated for predictor variables of log density, using linear least squares regression (R^2 = 0.41, Root MSE = 0.97, df = 4, 466), and including all estimates of 0 shrews km^{-2}.

Predictor variable	Regression coefficient			
	a	b	SE of a, b	β
Intercept	–5.135	–	0.885	–
Year of estimate	–	0.046	0.004	0.515
log Study area size	–	–0.768	0.141	–0.224
Elevation	–	–0.00081	0.000	–0.209
log Female body mass (kg)	–	–1.408	0.346	–0.164

log female body mass (slope, $b = 0.86$, df = 1, 475, $P < 0.05$). However, the small range of body masses in the sample rendered this regression as unreliable ($r^2 = 0.01$, Root MSE = 1.24).

As it has for other taxonomic groups, log density regressed on log study area size with a negative slope ($r^2 = 0.25$, Root MSE = 0.62, df = 1, 385, $P < 0.0001$; Fig. 2):

$$\log [\text{Density (N km}^{-2})] = 0.82 - 0.98[\log \text{Study area size (km}^2)] \quad (1)$$

Adding the estimates of 0 animals km^{-2}, which had not been possible for the order Carnivora, increased the standard error substantially ($r^2 = 0.21$, Root MSE = 1.10, df = 1, 475, $P < 0.0001$; Fig. 2, dashed line):

$$\log [\text{Density (N km}^{-2})] = -0.72 - 1.58[\log \text{Study area size (km}^2)] \quad (2)$$

Table 3 summarizes the best of many attempted multiple stepwise regression models of shrew density > 0. The standardized regression coefficient, β, indicated that the year of the estimate contributed most to the explanation of variation in shrew density (positive correlation), followed by study area size (negative correlation), female body mass (positive correlation), and the number of vegetation categories reported (positive correlation). These variables explained half the variation in log density of shrews.

Table 4 summarizes the best of many attempted multiple stepwise regression models of shrew density, including all the estimates of 0 shrews km^{-2}. The R^2 was lower and the Root Mean Square Error nearly doubled, but the raw data were probably more representative of real conditions. In this model, the year of the estimate was again the most contributive predictor variable of shrew density, followed by study area size, elevation (negative correlation), and female body mass.

The year of the estimate was confounded with how the site was chosen and continent (Fig. 3A and B), which themselves were strongly associated ($\chi^2 = 194$, df = 1, $P < 0.0001$). Randomly selected sites numbered 208 in North America and 82 in Eurasia, whereas sites selected for high density numbered 149 in Eurasia and only 3 in North America. Older estimates were mostly from randomly selected sites in North America, whereas more recent estimates were mostly from sites chosen based on prior knowledge of shrew presence in Eurasia. How the site was selected also related to study area size and the density estimate, where randomly selected sites averaged three times larger than those selected otherwise (Fig. 4). Smaller sites associated with higher density estimates (Fig. 4).

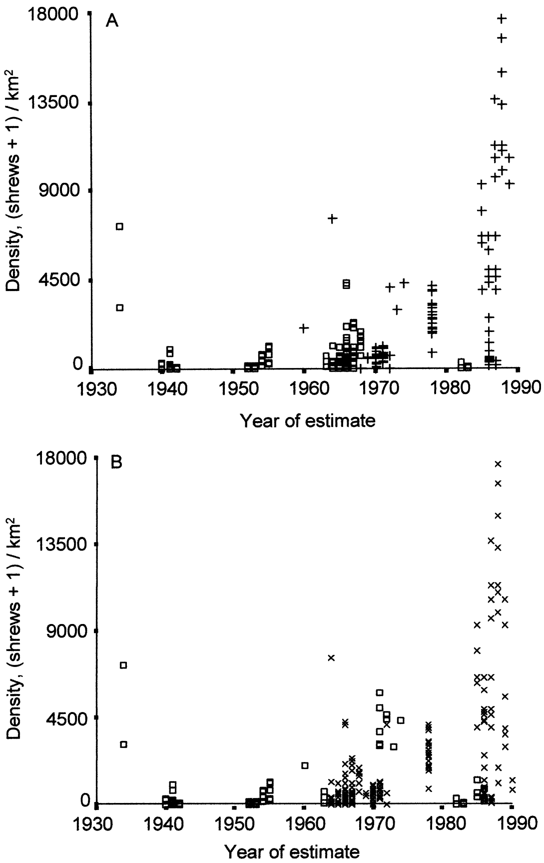

Fig. 3. Relationships between shrew density and year of study, and (**A**) whether study sites were selected randomly (squares) or based on prior knowledge of high density (crosses), and (**B**) whether they were in North America (squares) or Eurasia (crosses).

We compared the residual variation in log density from the multiple regression model that included estimates of 0 shrews km^{-2} with the remaining variables measured in this study (Table 5). Some significant relationships included higher densities for studies involving pitfall traps, for studies in broadleaf forest, and for studies on lands that are managed as game refuges and not

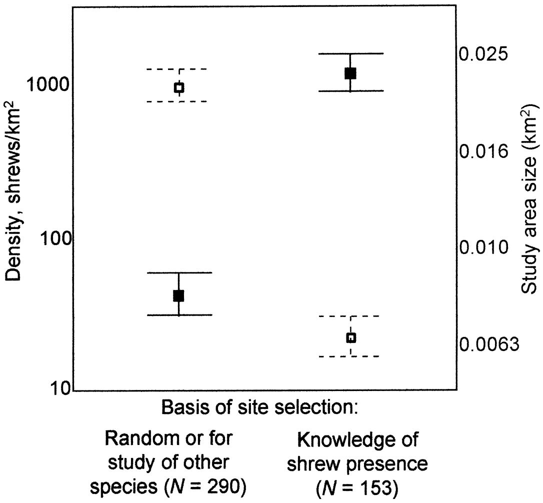

Fig. 4. The means and 95% confidence intervals of study area size (open square and dashed lines) and density (closed square and solid lines) compared by how the study site was selected.

subjected to livestock grazing. Also, kill and removal methods generated higher densities, as did studies focused on one species. Biologically significant lack of relationships were with species of *Sorex* (Fig. 5A), season (Fig. 5B), and latitude. The residual variation in log density also did not relate significantly to how the study site was selected, the type of estimator used, study duration, nor to the number of captures at the study site.

Compared with species of highly carnivorous Carnivora, log density of shrews related to log study area size almost as if shrews are smaller species of Carnivora (Fig. 6). Across orders, log density regressed on log study area size with a negative slope (r^2 = 0.92, Root MSE = 0.56, df = 1, 1366, P < 0.0001; Fig. 6):

$$\log [\text{Density (N km}^{-2})] = 1.02 - 0.85[\log \text{Study area size (km}^2)] \quad (3)$$

Based on the model of density regressed on study area size among species of highly carnivorous Carnivora (a = 0.825, b = –0.785), shrew density estimates averaged 1.5 and 2.5 times higher than predicted with and without inclusion

Table 5. Associations between field study attributes and the unstandardized residuals from the multiple regression model of density. Levels of significance are symbolized as follows: ns is P > 0.10; * is P < 0.05; and ** is P < 0.0001.

Variable	Smallest mean	Largest mean	Statistic	df
Continent	North America	Eurasia	$F = 2.10^{ns}$	1 460
Level of isolation	Mainland, contiguous	Island	$F = 0.03^{ns}$	2 460
Land use	Multiple-use land	Game refuge	$F = 10.6^{**}$	6 456
Site selection	Random	Based on presence	$F = 0.22^{ns}$	1 427
Sampling intensity	Capture-recapture	Kill and removal	$F = 2.63^{*}$	3 460
Estimation	guess and 0-capture	census	$F = 1.66^{ns}$	3 460
Study duration	Brief studies	Long-term studies	$r_p = 0.07^{ns}$	203
Type of trap	Snap trap	Pitfall trap	$F = 10.35^{**}$	5 460
Latitude	Lower latitude	Higher latitude	$r_p = 0.03^{ns}$	461
Female body mass	Larger animals	Smaller animals	$r_p = -0.07^{ns}$	461
Vegetation detail	Dominant species	All species listed	$F = 1.59^{ns}$	4 460
Dominant vegetation	Sage scrub	Broadleaf forest	$F = 7.12^{**}$	6 460
Relief	Mountainous	Hilly, foothills	$F = 7.68^{**}$	3 453
Season	Annual and winter	Summer	$F = 1.35^{ns}$	4 460
Month	January	December	$F = 1.51^{ns}$	11 431
No. species studied	19	1	$r_p = -0.13^{*}$	461
Livestock grazing?	Yes	No	$F = 12.68^{**}$	1 460
Hunting?	No	Yes	$F = 2.32^{ns}$	1 460
Timber harvest?	No	Yes	$F = 0.02^{ns}$	1 460
Number of captures	Few	Many	$r_p = 0.05^{ns}$	50
Map	Text description	Topographic map	$F = 8.06^{**}$	6 460

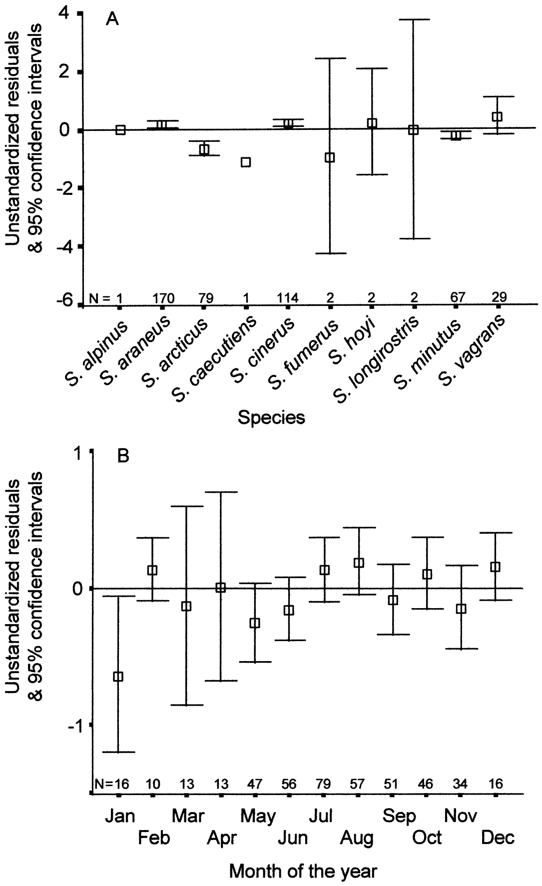

Fig. 5. The unstandardized residuals of log shrew density regressed on year of the estimate, log study area size, log female body mass, and elevation plotted against species of *Sorex* (**A**) and months of the year (**B**). Note that the value ranges differ between graphs **A** and **B**.

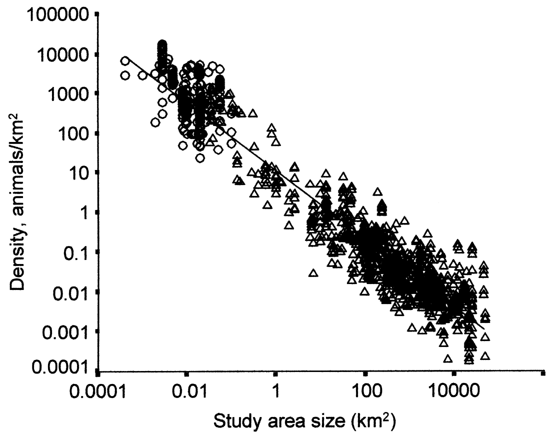

Fig. 6. Log density regressed on log study area size among species of *Sorex* (circles) and Carnivora (triangles).

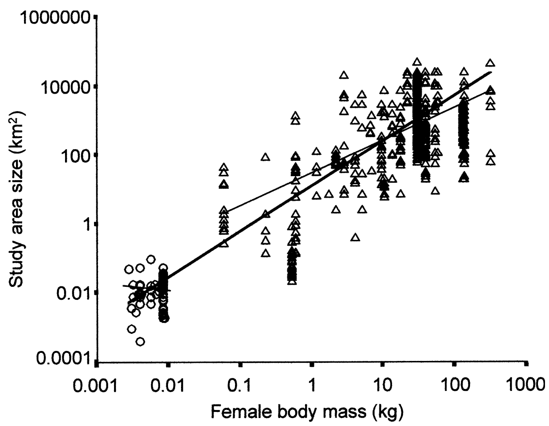

Fig. 7. Log study area size regressed on log body mass among *Sorex* (circles), Carnivora (triangles), and between orders (thick line).

of 0-values in the model (calculated as the backlogged difference between observed and predicted density estimates).

The size of shrew study areas did not increase with female body mass as it had among species of Carnivora (r^2 = 0.01, Root MSE = 0.36, df = 1, 475, $P < 0.05$; Fig. 7), but across both taxonomic groups log study area size regressed on log female body mass with a positive slope (r^2 = 0.84, Root MSE = 0.92, df = 1, 1479, $P < 0.0001$; Fig. 7):

$$\log [\text{Study area size (km}^2)] = 1.08 + 1.247[\log \text{Female body mass (kg)}] \quad (4)$$

The regression slopes between species of Carnivora with and without shrews were different (Analysis of Covariance, F = 619, df = 1, 1009, $P < 0.0001$). The model of study area size regressed on body mass among species of Carnivora (a = 1.471, b = 0.946) also predicted study area sizes for shrews that were 16.3 times larger than observed, on average. The mean and standard deviation of the number of carnivorous Carnivores was 68 ± 224, which was about 5 times the average number of shrews among the published estimates.

Discussion

In arriving at density estimates, some of the trends in study design observed for Carnivora were also observed for species of *Sorex*. However, important differences also emerged. Estimates of *Sorex* density involved briefer periods of time, an average of one fifth of the animals and a sixteenth of the study area size scaled to body mass. Vegetation was described in greater detail and with more distinct categories, perhaps because these details were deemed more critical to these smaller-bodied species. These trends expose important biases in animal population studies, affecting our interpretation of the spatial patterns of distribution across taxa (Smallwood *et al*. 1996).

The fact that shrew biologists conducted their studies in disproportionately smaller study areas, relative to functionally similar species of Carnivora, highlights the likely effect of investigator bias in designing studies. Relatively speaking, investigator choice in study area size appears to have been influenced by the typical body mass of the species (Fig. 7) and probably basal metabolic rate (McNab 1986). Whether the pattern of density among shrews is truly similar to that of Carnivora cannot be determined until much larger areas are used to estimate shrew density; the range of study area sizes would need to overlap between *Sorex* and species of Carnivora.

Other trends in study design were different between studies of *Sorex* and Carnivora. For example, no estimates of shrew density were made for the purpose of conservation or management, thereby buffering shrew studies from some of the ideological struggles that might influence the interpretation of many Carnivore density estimates (*see* Smallwood & Schonewald 1998). Also, nearly all estimates of shrew density relied on trapping, although none included reports of accidental shrew fatalities. Many of the studies used removal methods. These trends indicated less concern among shrew biologists for the effects of removing individuals on the resulting density estimate. Perhaps shrew biologists should be concerned about the removal of shrews because small mammal studies have revealed elevated densities of subadults who immigrated into the study area and filled vacated home ranges with multiple individuals (Sullivan *et al*. 1979).

In another example of different trends between shrew and Carnivore studies, density estimates of shrews were reported with less detail of physical relief, less information about the land use and surrounding landscape, less map detail, and less description of the condition of the population or the reliability of the estimate. These differences might also indicate an effect of scale. Perhaps shrew biologists see these study attributes as less important than do Carnivore biologists. However, these study attributes might be critical for interpreting shrew density estimates, and should be described in much greater detail by both shrew and Carnivore biologists. Biologists cannot understand the importance of these study attributes until they are fully described in an adequate number of published reports. Smallwood (1999b) recommends reporting methods for animal density estimates.

We explained a substantial amount of the variation in shrew density estimates using a relatively small set of measured variables (Tables 3 and 4), but we might have achieved better results had other variables been more consistently reported. We think that vegetation composition might have been a strong predictor of shrew density, as well as land use and physical relief. Shrews are commonly associated with wet, mossy areas. The most frequently occurring dominant vegetation complexes were evergreen forest (48%), grassland (20%), deciduous forest (24%) broadleaf forest (5%), and sage scrub (2%). However, vegetation and relief were reported too inconsistently and often too vaguely for them to contribute substantially to the explanation of variation in shrew density. The number of distinct types of vegetation described for the site correlated positively with shrew density (Table 3), but we do not know whether this correlation is driven by environmental complexity or is rendered spurious by greater attention to reporting detail correlating with density.

We were surprised by the lack of relationship of shrew density with season of the year, especially because shrews are an annual species and most estimates were tied to a month of the year, thereby providing us with high temporal resolution. In general, populations are thought to increase during late summer and early fall with the addition of the new cohort, then diminish as adults perish and juveniles establish territories. Our analysis did not agree — the months of highest density were December, February, and March. After considering other variables (Table 4), log density no longer varied significantly by season (month). The seasonal dynamics of shrew density are likely location-specific and could not be observed in our synthesis.

For explaining the variation in shrew density, the most important, inter-correlated suite of variables included the year of the estimate, how the site was selected, the continent of the study, and study area size. We found that randomly selected sites tended to cover larger geographic areas and gave smaller density estimates, whereas sites chosen for their known shrew presence were smaller and gave higher density estimates. The densities reported in the earlier North American studies were lower because the majority of them came from multiple species studies where the researcher(s) chose their study without knowing that shrews were present in abundance. Researchers in Eurasia often selected study sites because they knew their target species was present, sometimes in abundance. The tendency to select study sites based on species presence may be justified by time and budget constraints, but this approach sacrifices a broader representation of numerical distribution. Random or systematic site selection more accurately represents the frequency of shrew absence. It is important to report species absence. By doing so, biologists are better equipped to identify where potential gaps exist between populations; biologists better understand the spatial distribution and population structure of animal species.

We also found that densities between removal and intensive handling studies were close. Although accuracy cannot be determined by comparing estimates of density, the similar levels of precision among the sampling methods indicated that shrew biologists are applying them consistently. The high variation in density among the remote methods (i.e., guesses) can be owed to small sample size and the nature of the method alone. We suspect the variation in handling methods would decrease with a larger sample size, and a more clear trend would emerge showing that the level of handling would increase the density estimates, which would peak for removal methods.

Comparative studies have shown that pitfall traps are most effective at capturing shrews. Pucek (1969) reported a 10 times higher capture rate with pitfalls compared to snap and live traps in different vegetation complexes. We found little difference in mean density between pitfall and live traps until we factored in the variables listed in Table 4. Then pitfall traps generated significantly higher densities than did snap traps and live traps (Table 5). Again, accuracy of trap types cannot be determined by comparing density estimates.

Reliable density estimates are needed for calculations in studies of bioenergetics, mineral cycling, and population ecology (Smith *et al.* 1971). With the rise in monitoring and restoration efforts, the ability to compare population parameters becomes even more pressing. Based on our synthesis of published shrew densities, we believe that researchers could improve reporting of density and other study attributes to make them better suited for comparisons. We suggest that biologists adopt a standard and detailed method for reporting vegetation composition and spatial pattern on the study site, that the study site location be given in latitude and longitude, and that they report factors that might influence their estimates, such as trap injuries and fatalities, and how and why they selected the study site. More research is needed to account for variation in shrew densities. We recommend studies spanning larger areas and longer periods and involving many of the other shrew species for which no estimates of density have been published. We may never develop a method to accurately determine density, but by explaining the variation in density, we may improve our accuracy a great deal.

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