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SPOTTED OWL ECOLOGY: THEORY AND METHODOLOGY—A REPLY TO ROSENBERG ET AL.

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In their remarks on the study of Spotted Owls (*Strix occidentalis*) by Carey et al. (1992). Rosenberg et al. (1994) questioned the appropriateness of certain analyses and methods, and specific interpretation of the results. Herein, I respond to the comments of Rosenberg et al. (1994), which are summarized in italics.

Sample sizes were nor clear. Twenty 20-ha grids (11 in old, 9 in young forest) and 27 4-ha transects (young forest) in Oregon and 14 20-ha grids (6 in old, 8 in young forest) in Washington were trapped (Carey et al. 1992:225—228). Only woodrats (*Neoroma* spp.) were trapped on transects. The 20 Oregon grids were trapped 1—9 seasons each; for the 16 trapped $\geq$ 3 times, each season was reported (Carey et al. 1992:Table 5); 80 estimates of flying squirrel (*Glaucomvs sabrinus*) densities were made.

T test vs. ANOVA. Densities of flying squirrels in young and old forests were compared by (1) a paired *t* test of mean densities over seasons and years (a test of the null hypothesis that difference in mean density = 0 over time); (2) grand (mean of seasonal means for each stand) means and standard errors (which allows an impromptu *t* test, doubling the standard error to determine difference at $P < 0.05$): and (3) box-and-whisker plots of densities by age class and season for 5 yr (Carey et al. 1992:Fig. 4). Other tests (ANOVA and Kruskal-Wallis), not presented, showed the same results. Therefore. Carey et al. (1992) presented the simple, robust test of means of means. Even so, I prefer box-and-whisker plots because they are more informative than *F*, *t*, and *P* values. These plots allow the reader to compare maxima, third quartiles, interquartile ranges, ranges, and medians of distributions of densities, e.g., the interquartile ranges in old forests are greater than those in young forests, perhaps reflecting that there are two types of populations in old forests, those that have been subjected to intense foraging by Spotted Owls and those that have not. Additionally, where >2 stands were sampled in each age class (four seasons in 3 yr), there was no overlap of interquartile ranges of densities in old and young forests (Carey et al. 1992:Fig. 4).

I consider these analyses to be robust because (1) results span 5 yr; (2) stands were sampled intensively (Carey et al. 1991): (3) all available blocks of old forest and young forest in the landscape were sampled; (4) the full range of elevational and longitudinal variation in the southwestern Coast Range (including the adjacent valley margins and Klamath Mountains) and the Olympic Peninsula were incorporated into the estimates; (5) even the effects of intense foraging by Spotted Owls were included in the estimates for old forests; and (6) statistical tests and graphical analyses still demonstrated higher squirrel densities in old forest than in young forests. The objective of the comparison was to determine if densities of flying squirrels in young and old forests supported a hypothesis that Spotted Owls preferentially select old forests for foraging because the squirrel is most abundant there. Measures of postforaging densities could be, therefore, legitimately excluded from the comparison; if they had been excluded, mean densities for old forest would have been even higher than those reported.

Rosenberg et al. (1994) state that the paired *t* test "seems inappropriate because it ignores variability ... difference in sampling intensity ... and does not allow for lack of independence...." The test was used to examine consistency among seasons. The samples in each season were composed mostly of the same stands and were taken to represent the mean for two age classes in the landscape. The test capitalizes on the benefits of using means (normally distributed according to the central limit theorem) and pairing (equal variances are not required between the two samples). Dowdy and Wearden (1983:180) state "using a matched-pair design is a way to control extraneous variability." The use of the paired *t* test by Carey et al. (1992) is analogous to a repeated-measures ANOVA (Zar 1984:222), i.e., repeated measures of the mean densities of squirrels in two age classes of forests in the same landscapes.

Density estimators for flying squirrels. Rosenberg et al. (1994) report that Carey et al. (1992) inappropriately mixed minimum number known alive (MNKA) and modified Lincoln-Peterson (MLP) estimators and used MNKA if <10 individuals were caught. Rather, Carey et al. (1992) used MNKA for total captures (of all individuals) <10, an arbitrarily chosen small number that covered the few cases when application of the MLP would have been gratuitous. Of the 80 estimates for Oregon, 77 were calculated by MLP The MLP for the other three were the same as the MNKA. On the Olympic Peninsula, 29 estimates were made for 14 stands (1-3 yr per stand, all but one sampled at least twice); 10 were 0 (no captures of flying squirrels in 1600 trap nights); 11 were based on captures <I 0. Only in one young stand was MNKA < MLP (3 vs. 5); the estimate of five squirrels was used.

Studying low-density populations is not desirable statistically, but biologists must face "biological reality" (Montgomery 1987). The MLP is recommended

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for low-density populations (Menkens and Anderson 1988) and produced lower coefficients of variation (cv) than more complex estimators when applied to data on flying squirrels (Carey et al. 1991). Grids were as large as possible, traps were numerous (200 traps/grid), and probabilities of capture were >0.80 with 6-8 nights of trapping.

Grids vs. transects. Rosenberg et al. (1994) report that data from grids and transects were inappropriately combined and that comparisons of woodrat abundances among forest types were suspect because long transects sample within-stand variation better than grids. Comparisons of abundances among forest types (vegetation zones), however, were based only on grid-based mark—recapture trapping. Data from grids and transects were never combined; mean MNKA densities of woodrats for categories of forest that were trapped with different methods were compared (Carey et al. 1992:Table 4). The contention that transects sample stands better than grids is wrong; grids and transects designed to sample entire stands both provide complete coverage.

Flying squirrel densities are higher in old forest. Rosenberg et al. (1994) report that the conclusion that flying squirrels were more abundant in old forest than in young forest was not supported by the data presented because ≥2 young stands were sampled "in only five of nine sampling periods." This is true, but the number of samples was large compared to other studies of the flying squirrel, e.g., Rosenberg and Anthony (1992) took only 20 samples in two periods. I reanalyzed Carey et al.'s (1992) Oregon data, using only spring results with $n \geq 3$ in each year and age class (19861988: 17 estimates from old. and 11 from young, stands), with a two-sample t test ($t = -7.75$, df = 4, $P = 0.001$) and found the same difference in means (1.0 squirrel/ha)' reported in the original analysis. Additionally, Rosenberg et al. (1994) claimed that the results reported by Carey et al. (1992) were not supported by "data from other parts of the Northern Spotted Owl's range." Specifically, they cite Rosenberg and Anthony (1992). Rosenberg and Anthony (1992), however, stated their own results were "in contrast ... others have suggested that northern flying squirrels are more abundant in old-growth than in second-growth forests (Harris and Maser 1984; Brown 1985; Franklin 1988)." Volz (1986) and Witt (1992) also differ with Rosenberg and Anthony (1992). Carey (1995) reanalyzed data from Rosenberg and Anthony (1992) and, after correcting for variance in grid shape and for possible predation by Spotted Owls, found the same l squirrel/ha difference between old and young forest that Carey et al. (1992) reported.

Owls depress flying squirrel densities. Carey et al. (1992) asked if abundance of flying squirrels decreases with intense foraging by Spotted Owls. i.e., do the data support prey depletion or not. For each of I 1 old Douglas-fir (*Pseudotsuga menziesii*) stands studied for 2—4 yr they calculated, by season, the hunting pressure of the previous year and the present density of flying squirrels. Hunting pressure was calculated in owl-year based on the proportion of independent relocations of each owl using each of the old stands. Only relocations ≤ 1 km from the centers of trapping grids were counted (Carey et al. 1992:233), a standardization necessary, but not, as Rosenberg et al. (1994) claimed, omitted. Rather than the single graph that Rosenberg et al. (1994) refer to, the analysis consisted of presenting (1) data showing the flying squirrel was the primary prey in the areas at the time; (2) examples of variation in squirrel densities over time relative to owl nesting (and concomitant intensive use), showing reduced abundance following nesting, followed by recovery. while stands without predation did not show similar declines; and (3) box-and-whisker plots of squirrel densities by three categories of owl hunting pressure that showed an inverse relationship between hunting and density (Carey et al. 1992:Figs. 5, and 6c, d). The box-and-whisker plots (Carey et al. 1992:Fig. 5) showed clear separation of the third and first quartiles of density after light and heavy foraging activity, respectively. Median density under light predation was twice that under heavy predation. The data were supportive of prey depletion; Carey et al. (1992) concluded "... moderate to high foraging activity ... appeared to depress flying squirrel populations." To me. the use of "appeared" distinguishes this statement as an explanation of an observed phenomenon rather than a statement of fact (effect).

Squirrel densities are more variable in young stands. Rosenberg et al. (1994) state that the conclusion that flying squirrel abundance was more variable in young than in old stands was not supported by data. Means, standard errors, and sample sizes (n) for seasonal abundance were provided (Carey et al. 1992); cv calculated from these data are 54% for young stands and 15% for old stands.

Fragmentation affects flying squirrels. Rosenberg et al. (1994) report that Carey et al. (1992) made an unwarranted claim and provided the quotation: "Fragmentation of old forest does reduce overall numbers of flying squirrels. Stands intensively managed for timber, recent clear-cuttings, and conversion of forest to nonforest did isolate flying squirrel populations." What was actually written as a discussion of results was (in summary): ". . . we cannot conclude that fragmentation due to past timber harvesting in Oregon isolated populations of flying squirrels [in general] ... Fragmentation of old forest does reduce overall numbers of flying squirrels [i.e., through loss of habitat] ... stands intensively managed for timber, recent clear-cuttings, and conversion of forest to nonforest did isolate flying squirrel populations [in specific instances]. Clear-cutting was extensive…."Flying squirrels were found in extensive stands of second-growth forests and in forests surrounded by fields, clearcuts, and young stem-exlusion phase stands that did not contain flying squirrels (these latter populations were indeed isolated); 28—41% of the landscapes were in nonforest or stand initiation stages (Carey et al. 1992:Table 7). Types of fragmentation that resulted in small, isolated stands of old forest were illustrated (Cagey et al. 1992:Fig. 2) and described extensively (Carey et al. 1992:237─240).

Patterns of abundance of woodrats. Rosenberg et al. (1994) state that conclusions about patterns of abundance of woodrats are opposite of the patterns that are present in the data; specifically, the authors dispute: (1) that bushy-tailed woodrats (*N. cinerea*) were moderately abundant in some old Douglas-fir forests in some years; (2) that bushy-tailed woodrats were generally absent from young Douglas-fir forests; (3) that occupancy of old Douglas-fir forests was variable. suggesting local extinctions; and (4) that occupancy of early seral stages of mixed-conifer forests by dusky-footed woodrats (*N. fuscipes*) was variable. I believe their comments result from not distinguishing between conclusions about woodrats in Douglas-fir vs. mixed-conifer forests, upland vs. streamside forests, and bushy-tailed vs. dusky-footed woodrats (Carey et al. 1992:Tables 4 and 5). Rosenberg et al. (1994) rank abundances of bushy-tailed woodrats by selectively mixing data (using only the highest values for stand conditions) from mixed-conifer and Douglas-fir forests, whereas Carey et al. (1992) emphasized the interaction of vegetation zone, stand condition, and woodrat abundance. For example, among the stand conditions studied in each zone, bushy-tailed woodrats were most abundant in streamside forests: streamside densities in mixed-conifer forests were 4 times those in Douglas-fir forests, and many other stand conditions in mixed-conifer forests had higher densities than Douglas-fir streamside forests. In Douglas-fir forests, only streamsides were consistently occupied by bushy-tailed woodrats. To rebutt Carey et al.'s (1992) statement that occupancy of early seral stages of mixed-conifer forests by dusky-footed woodrats was variable, Rosenberg et al. (1994) calculated cv (dividing the standard error by the mean) for bushy-tailed woodrats and duskyfooted woodrats in different stand conditions. Had they calculated cv by multiplying the standard error by $\sqrt{n}$ and dividing by the mean, they would have found that the cv for the density of dusky-footed woodrats in managed, mixed-conifer pole stands was 110% and that the variance was greater than the mean, suggesting a contagious (clumped) distribution. i.e., variable occupancy. Other cv are irrelevant. I believe Carey et al. (1992) presented data that adequately support their conclusions. More data could have been presented, as asserted by Rosenberg et al. (1994); for example, Table 5 (Carey et al. 1992) was condensed from two larger tables, at the request of the editor (to save space).

Rosenberg et al. (1994) also state that the habitat associations of woodrats (Carey et al. 1992) were not supported by other studies. I know of no other studies of bushy-tailed woodrats in Oregon. Studies of dusky-footed woodrats in Oregon and northern California report results similar to Carey et al. (1992), see Carey (1991) for a review, including Sakai and Noon (1993), who also report bimodal distributions of dusky-footed woodrats (high numbers in very young and very old stands).

Rosenberg et al. (1994) dispute the contentions that fragmentation could negatively affect bushy-tailed woodrats and that streams might be the avenues for recolonization of vacated habitat. Carey et al. (1992) showed (1) that Spotted Owls preferentially select old forest for foraging, that bushy-tailed woodrats are an important component of the owl's diet, and that bushy-tailed woodrats sporadically occupy old Douglas-fir forests; (2) that bushy-tailed woodrats rarely occupy young, upland, Douglas-fir forest; and (3) that fragmentation has resulted in isolated blocks of old forest in the home ranges of Spotted Owls (i.e., more discrete hunting patches). Escherich (1981) reported that bushy-tailed woodrats are prone. because of their social system, to extirpation by predators; Carey et al. (1992) showed bushy-tailed woodrats had the same social system in Oregon. Carey et al. (1992) concluded that bushy-tailed woodrats in old forests and streamside forests were isolated by young upland forests. They also concluded that virtual absence from young forests but regular, although sporadic, occurrence in old forest, is indicative of a fragmentation effect, i.e., old forest fragmented by young forest. Consistent occupancy and high densities of bushy-tailed woodrats in streamside forests suggest that streamsides could be avenues for recolonizing old forests after a local extinction due to predation, death from other causes, and stochastic demographic processes.

Area of old forest used by Spotted Owls is inversely related to prey biomass. Rosenberg et al. (1994) state that the reported relationship between home range and biomass (Carey et al. 1992) was unfounded because regional (vegetation zone) estimates of biomass were based on different techniques and estimates of error were not provided. Carey et al. (1992) related area of old forest used, not home range size, to prey biomass. Home range size was shown to increase with forest fragmentation; area of old forest used remained relatively constant within vegetation zone. To examine prey abundance and area of old forest used. Carey et al. (1992) calculated the mean biomass of medium-sized prey in old forests and plotted that against the mean amounts of old forest used by Spotted Owls as determined by them or Thomas et al. (1990). Only data from grid-based mark-recapture trapping were used; transects were not placed in old forests (Carey et al. 1992:228). Mean biomass values, ratios of biomass, and ratios of areas used among zones were reported (Carey et al. 1992:235). They concluded that "Area of old forest used decreased with increasing biomass of prey (Fig. 8)" and did not believe any more precision (e.g., a predictive equation) was warranted because they had only three locations and the relationship seemed curvilinear. Estimates of error (variance) for prey densities and amounts of old forest used in southwestern Oregon were provided (Carey et al. 1992:233─234, Table 9). Variances of biomasses were not provided because biomass was the simple product of the multiplication of mean density by mean body mass for each species of prey. Variances for amounts of old forest reported by Thomas et al. (1990) were not provided.

Discussion. Rosenberg et al. (1994:1512) introduced their comments by referring to six hypotheses about use of old forests by Spotted Owls and stating that the validity of Carey et al.'s (1992) conclusions is "critical to ... land managers ... interested" in using silviculture to benefit Spotted Owls. Carey (1985) formulated and presented the six hypotheses. These hypotheses are comprehensive, but not mutually exclusive (Carey 1985:105─107). Indeed, Gutierrez (1985), in a recapitulation. combined the prey abundance and prey availability hypotheses. Rosenberg et al. (1994) interpret those two hypotheses as exclusive and the prey availability hypothesis as suggesting that prey are more efficiently hunted in old forests because owls can forage more easily through open understory than developed understory. These interpretations underlie their conclusions of uncertainty about the value of increasing carrying capacity for prey and the use of silviculture to create Spotted Owl foraging habitat (Rosenberg et al. 1994:1515). The prey availability hypothesis, however, actually implies that multilayered vegetation in old growth provides an array of hunting perches from the canopy to the forest floor that, along with the patchy nature of the understory, allows the owls to more effectively exploit the prey base (Carey 1985). Most young stands (e.g., 35─70 yr old) are in the stem exclusion stage of forest development, which is characterized by lack of understory. Old growth is defined as having well-developed understory (Old-Growth Definition Task Group 1986), as are stands used by Spotted Owls (Thomas et al. 1990, Carey et al. 1992). Young forests in which owls forage have a more fully developed understory than old forests do, on average, and than young forests do, in general (Carey et al. 1992: 247). Rosenberg et al. (1994:1515) imply owls do not forage in young forests. But all studies of owl foraging to date report use of young forests (Thomas et al. 1990). Recent analyses (Carey 1995) show a positive relationship between understory development and the abundance of northern flying squirrels. Thus, understory development may contribute to increased numbers of flying squirrels, improve the ability of Spotted Owls to prey on the squirrels, and provide roosts for Spotted Owls (Carey et al. 1992:232).

Some of the critique by Rosenberg et al. (1994) reflects philosophical differences about the value of exploratory vs. experimental studies, of the value of statistical tests vs. graphical presentations of data, and of the nature of the scientific process. I believe that exploratory techniques such as box-and-whisker plots are more heuristic than simple statistical tests, especially when, as in most field studies, the results of statistical tests are only heuristic (Quinn and Dunham 1983). The scientific process begins with review of the literature and formulation of questions (or hypotheses) and ends by placing those results back into the common understanding of natural phenomena, as in the theory-practice iteration of Box (1976:792): ". . . the scientist must be, as it were. mentally ambidextrous; fascinated equally on the one hand by possible meaning. theories, and tentative models to be induced from data and the practicality of the real world. and on the other with the factual implications deducible from tentative theories. models, and hypotheses." If the scientist does not induce and deduce. then those who would use the research, must (see Thomas et al. 1990).

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