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Can We Infer Habitat Quality From the Results of Wildlife Surveys?

2000 Final Report

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Executive Summary

Management plans for Pacific Northwest (PNW) forests rely heavily upon species-habitat association data to establish the quantity and types of habitat required to meet conservation objectives. For birds, such associations are typically determined by relating a species' relative abundance (derived from point-count surveys) or density (derived from spot mapping) to a series of habitats. Actual measures of avian productivity (numbers of young fledged from nests) or nesting success (probability of nest survivorship), which are presumably much better indicators of habitat quality, are rarely made, however. To test the assumption that relative abundance and density of breeding birds in PNW forests are reliable measures of habitat quality, we conducted a two-year study (1998–1999) in managed forests of the southwest Cascade Mountains of Washington. Our work was initiated in direct response to a request for proposals issued by Washington State Department of Natural Resources in 1997.

Specifically, we addressed the following two research questions and hypotheses: (i) What are the relationships between relative avian abundance and density as derived from traditional point-count survey and spot-mapping techniques, respectively, and how do these parameters correlate with habitat quality as measured by reproductive success? Our null hypothesis was that avian abundance, density, and reproductive success are highly correlated across commonly occurring managed forest conditions; and (ii) Based upon meta-analyses of data collected in forest types of the southwest Cascade Mountains of Washington, as well as elsewhere in the PNW (east-central Washington, northeast Oregon, and west-central Idaho), for which species (or species' guilds) is relative abundance likely to be a misleading indicator of habitat quality? Our null hypothesis was that avian abundance and density are accurate measures of habitat quality throughout managed forests of the PNW.

Point-count surveys, spot mapping, and nest monitoring were simultaneously conducted in each of four replicates of three different forest treatments in each year: (1) 8- to 12-year-old managed forest (early seral); (2) 40- to 60-year-old managed forest (mid seral); and (3) 150- to 270-year-old naturally regenerated old growth forest (late seral). Point-count surveys yielded 9,429 individual bird detections representing 72 species. Spot mapping resulted in territory maps for 14 bird species. Efforts to find and monitor nests resulted in 681 nests of 40 bird species. In 1999, to improve our ability to interpret apparent discordance among abundance, density, and reproductive success for some bird species, we also collected behavioral data by conducting focal observations on the Winter Wren and Song Sparrow in a subset of forest stands. This small component of the larger study was intended to help us better understand why

point-count surveys may not provide reliable measures of population status and viability for some species in some forest treatments.

To address the first part of research question (i), we initially examined relationships between measures of relative avian abundance and bird density. Relative abundance was calculated using field data collected at six different point-count radii (15-, 25-, 50-, 75-, and 100-m radii, and unlimited distance counts). Density estimates were derived in two ways: (1) from spot-mapping data; and (2) using the software program DISTANCE. Correlation analyses between these measures of abundance and density revealed significant positive correlations for the majority of species and species' guilds (or groups). Specifically, point-count surveys were apparently very good indicators of density (derived from spot-mapping) for the Dark-eyed Junco, Orange-crowned Warbler, and Winter Wren. In contrast, density of Brown Creeper, Hermit/Townsend's Warbler, and Varied Thrush was generally uncorrelated with abundance. Compared with density calculated using spot maps, DISTANCE estimates of density were more highly correlated with relative avian abundance and significantly different from measures of density derived from spot mapping for approximately 50% of species and species' groups. Regardless of which density measure we analyzed, however, the correlation with relative avian abundance sampled at small detection distances (i.e., 15- and 25-m point-count radii) tended to be low and highly variable, suggesting that either birds were responding to the observer, or that the sample area was too small to get reliable estimates. Only when we examined detection distances of 50 m and greater did we find consistently high (statistically significant) correlations between abundance and density, and it was at the 50-m radius distance that we found variance among species-specific correlation coefficients to stabilize.

To address the second part of research question (i), we calculated the following three measures of reproduction for as many species as possible: (1) productivity per nest (number of young fledged per nest); (2) nest success (Mayfield estimates of nest survivorship); and (3) productivity per unit area (number young fledged per 32 ha study plot). These variables, presumed to better reflect habitat quality, were then correlated with relative avian abundance and bird density. Per-capita reproduction refers to those measures of reproductive effort that are calculated on a per nest or per bird-pair basis. That is, the individual nest (or bird-pair) is the unit of measure upon which mean values of reproductive success are calculated within each sample study plot. Both nest-level productivity and Mayfield nest success are types of per-capita reproduction.

Per-capita reproduction can be used to infer habitat quality as long as bird species do not exhibit density dependent nesting behavior (i.e., as long as nest numbers increase with increasing bird numbers). For most species, per-capita reproduction (i.e., productivity per nest or Mayfield nest success) was either density independent (e.g., American Robin, Song Sparrow) or inversely density-dependent (e.g., Willow Flycatcher, Winter Wren). Such relationships suggest that habitat quality can likely be inferred from point-count surveys as long as nest numbers also increase with bird numbers (an assumption supported by our data). For three species, however (Chestnut-backed Chickadee, Varied Thrush, and Pacific-slope Flycatcher), we found density dependent nest-level reproduction; for these species, we conclude that point-count surveys would be unreliable since habitat quality would be highest (i.e., nest-level productivity and survivorship would be high) where abundance or density was lowest, and vice versa.

Although more difficult to estimate than per-capita reproduction, a more indicative measure of habitat quality is area-level productivity. Correlation analyses among abundance, density, and area-level productivity yielded results that suggested habitat quality could be reliably inferred from point-count surveys or assessments of density for six of 11 species examined (Brown Creeper, Chestnut-backed Chickadee, Dark-eyed Junco, Song Sparrow, Willow Flycatcher, and Winter Wren). Of the five species for which area-level productivity was uncorrelated with abundance and density, the Varied Thrush and Pacific-slope Flycatcher had very low correlations; it is for these two species in particular, therefore, that we question the reliability of survey-type data for habitat quality assessments. Notably, we found no significant negative correlations between area-level productivity and relative abundance or density for any species. Such a result would have been troubling because it would have suggested that survey data were highly misleading, inferring that the lowest quality habitat was in fact the highest, and vice versa. With the exception of aerial-feeding birds, guild-level analyses revealed significant positive correlations among abundance, density, and area-level productivity in all cases. For researchers and/or managers interested in assessing forest quality for breeding bird communities as a whole, we conclude from our analyses that survey techniques, such as point counts and spot mapping, would yield reliable data when area-level productivity is used as the measure of reproductive success. We did find area-level productivity to be more highly correlated with density than with relative abundance, which would imply that if researchers could not measure reproductive success, spot mapping would be a better option compared to point counts.

To examine effects of forest treatment on relationships between abundance and productivity, we also compared slopes of treatment-specific regression lines between relative avian abundance and area-level productivity for five bird species and all species' groups. Although we found no statistically significant differences between forest treatments, our comparisons revealed some strong trends and potentially troublesome patterns. In some cases (e.g., American Robin, Brown Creeper), the relationships between abundance and habitat quality (as measured by area-level productivity) were in direct contrast with one another, depending on forest treatment. Such results imply that many birds on point counts in one forest treatment means something very different from many birds on point counts in another forest treatment. If these observed patterns are indeed real, the implications for bird conservation and habitat management are clearly enormous. Despite the lack of statistical significance, we urge researchers in the future to be aware of the potential for measures of abundance and density to be misleading indicators of habitat quality for some species in some habitats.

Pooling data from the southwest Cascade Mountains of Washington with similar data from three other regions of the Pacific Northwest (east-central Washington, northeast Oregon, and west-central Idaho), we addressed our research question (ii) by conducting "meta-analyses" on 26 species, 10 species' groups, 6,275 individual birds, and 936 nests from 31 study plots. Consistent with our findings from data collected only in southwestern Washington, avian abundance was uncorrelated with per-capita reproduction for the majority of species and species' groups. In most cases, therefore, we believe that quality of forests throughout the Pacific Northwest could be reliably inferred from measures of abundance. Exceptions included Red-breasted Nuthatch, Warbling Vireo, Western Tanager, and Pacific-slope Flycatcher. We also examined region-specific and harvest-intensity-specific relationships across the Pacific Northwest to determine whether the reliability of survey data might vary with region and forest treatment, respectively. For most bird species and/or species' groups across the Pacific Northwest, region and harvest intensity did not influence relationships between abundance and reproduction. For some species or species' groups, however, region (e.g., Dusky Flycatcher, resident birds, foliage-gleaning birds) and harvest intensity (e.g., Winter Wren, cavity-nesting birds) were important factors that appeared to influence relationships between abundance and reproduction. The implication of these findings for our study is that survey techniques may work well in some regions and some forest conditions for some species, but not necessarily in all of them.

Finally, our focal observations generated >24 hr of behavioral data (broken down to the nearest second) for a total of 33 independent 30-min observation bouts on Winter Wrens and 16 independent 30-min observation bouts on Song Sparrows. The vocalization study suggested that while Winter Wren vocalization rates can be quite variable, there was little evidence to suggest that singing duration or song counts varied by treatment type. The best predictor of song rates in Winter Wrens and Song Sparrows was territory status, although the two species show opposite patterns. Vocalization rates for territorial Winter Wrens were nearly half the rate for nonterritorial wrens, while vocalization rates for territorial Song Sparrows were nearly twice the rate of nonterritorial sparrows. High numbers of nonterritorial Winter Wrens in some stands suggested that nesting phenologies were not synchronized among stands.

In conclusion, and perhaps as one would have predicted, we report mixed results with respect to the use of surveys to reliably infer habitat quality. In general, habitat quality for most bird species, when considered separately, collectively in guilds, or as an entire bird community, appears to be adequately assessed via standard point-count survey and spot-mapping techniques as long as the appropriate measure of avian reproductive success is used in analyses. In all of our analyses, however, there were always some bird species and/or species' groups for which surveys did not reliably measure habitat quality. Moreover, these cases often were consistent from one analysis to another, and sometimes dependent on forest treatment and/or geographic region. We therefore believe that our data from the southwest Cascade Mountains of Washington, and elsewhere in the Pacific Northwest, provide sufficient evidence to justifiably question the broad-scale use of bird surveys to assess forest quality. Researchers and wildlife biologists must be aware of the limitations of their data and we urge them to go beyond the traditional survey approach whenever possible, especially if resulting data are to be used to make important management decisions.

Glossary of Terms

Area-level productivity

The number of young fledged per unit area. We made the assumption that each territory mapped for a species contained a nest and calculated area-level productivity by multiplying territory numbers by the mean number of young fledged per nest across all nests in a study plot.

Density dependent reproduction

A relationship where reproductive success decreases as the number of birds per unit area in the population increases.

Density independent reproduction

A relationship where reproductive success remains constant as the number of birds per unit area in the population increases.

DISTANCE software program

DISTANCE is a Windows-based computer package that allows you to design and analyze distance-sampling surveys of wildlife populations. For our project, we used DISTANCE to estimate bird density from point-count data. A number of assumptions must be considered, as well as recording distances to individual detections. See the DISTANCE website at http://www.ruwpa.st-and.ac.uk/distance/distanceabout.html for more details.

Hypothesis

A provisional theory set forth as a testable relationship between avian abundance, density, and reproductive success.

Inverse density dependent reproduction

A relationship where reproductive success increases as the number of birds per unit area in the population increases.

Mayfield nest success

Based upon Mayfield (1975), this is the probability that a nest will survive to successfully fledge one young of the host species.

Meta-analysis

An analysis of data collected during multiple independent studies conducted over a large geographic region (the Pacific Northwest states of Washington, Oregon, Idaho, and Montana).

Nest-level productivity

The mean number of young fledged per nest, calculated by species and study plot.

Per-capita reproduction

Measures of reproductive effort that are calculated on a per nest or per bird-pair basis. That is, the individual nest (or bird-pair) is the unit of measure upon which mean values of reproductive success are calculated within each study plot. Both nest-level productivity and Mayfield nest success are types of per-capita reproduction.

Point-count bird surveys

Standardized sampling protocols that measure relative avian abundance by counting the number of individual birds by species seen and/or heard at a given location during a given period of time, usually with a predetermined sample radius.

Spot-mapping bird surveys

Standardized sampling protocols that measure bird density directly in the field by repeatedly mapping the locations of individual birds during a single breeding season and thereby estimating territory boundaries and numbers per unit area.

1. General Introduction

"*Can we infer habitat quality from the results of wildlife surveys?*" To ask this question is critically important; to answer it is absolutely essential. Our knowledge of species-habitat associations in forests of the Pacific Northwest (PNW) has improved throughout the past decade (e.g., Ruggiero et al. 1991 and references therein, McGarigal and McComb 1995, Carey and Kershner 1996, Hagar et al. 1996, Aubry et al. 1997, Hallett and O'Connell 1997, O'Connell et al. 2000, Pearson and Manuwal 2001, Sallabanks et al. 2001a). Unfortunately, however, the link between measures of abundance of wildlife species and their population viability has not been firmly established in any of these studies. Inferences about the actual quality of habitat can only be indirectly deduced from correlational and often poorly replicated wildlife surveys, and yet a recent review by Sallabanks et al. (2000a) indicates that such studies are the norm. Studies of species-habitat associations are known to be limited for numerous reasons (Wolff 1995), yet few research biologists have critically questioned the relationships between the factors typically measured in such studies (i.e., relative abundance or density) and habitat quality (as indicated by reproductive success, for example). Numerous studies, mostly on birds, have noted that density is not necessarily an accurate indicator of habitat quality (Krebs 1971, Van Horne 1983, Pulliam 1988, Robbins et al. 1989, Gibbs and Faaborg 1990, Blake 1991, Martin 1992, Vickery et al. 1992a, Hagan et al. 1996, Lautenschlager 1997, R. Sallabanks, *unpubl. data*).

There is clearly sufficient evidence to question the assumption that high population density, presumably a result of more abundant resources, also will reflect greater reproductive success and therefore better habitat quality. Our study addressed this assumption directly and therefore has great significance for the conservation of wildlife populations in managed forests of the PNW and elsewhere. Moreover, by addressing the question, "*Can we infer habitat quality from the results of wildlife surveys?*", we also can address some of the concern that the scientific and management communities have about the ecological value of managed forests. To achieve our objectives, we chose to work with forest avifauna (see below).

This document reports on our two-year study (1998–1999) in the southwestern Washington Cascades. We measured two commonly used abundance estimators (relative abundance and density) and productivity (numbers of young fledged) of forest bird species in three treatment types (regenerating clearcuts, commercially thinned managed forest, and naturally regenerated old growth forest). From these data, we then generated six measures of relative avian abundance, two measures of density, and three measures of reproductive success (see below) for further analysis. Landscape variables were controlled to the extent possible. Our intent was to use these data to determine which abundance estimator was the most reliable indicator of habitat quality. Our approach was to answer the questions posed in the Scope of Work outlined in Washington State Department of Natural Resources (DNR) Request For Proposals (RFP) No. 98-037 as detailed below. We begin this report by reviewing our specific research objectives, scientific rationale, experimental design, and sampling methods before presenting results and interpretation.

1.1. Why Use Birds?

We chose to address the question of whether habitat quality can be inferred from the results of wildlife surveys by focusing on forest birds. There are many reasons for choosing birds to answer this question, including the following: (1) results will have broader implications because birds have been studied more frequently than other taxa (i.e., a greater number of past studies can be evaluated); (2) data will be more rigorous (greater sample sizes, less variance, more power) because the relative abundance, density, and reproductive success of birds are relatively easy to measure compared with other taxa (e.g., small mammals, amphibians and reptiles); (3) birds are typically used as indicators of forest and ecosystem health and the viability of other wildlife populations (e.g., Terborgh 1989, Wilcove 1994, Martin 1995); (4) birds are known to be sensitive to changes in habitat quality that might occur as a result of forest management (Sallabanks et al. 2001b and references therein, R. Sallabanks, *unpubl. data*); (5) the relationships among abundance, density, and reproductive success can potentially be evaluated for more species than if other taxa were studied; (6) there are more threatened and endangered species of birds than other taxa, and recent trend analyses (e.g., Sauer et al. 1997) indicate some avian populations are declining; (7) common bird census techniques (e.g., point counting) are relatively indirect, compared to mammal and amphibian trapping, for example; and (8) earlier studies of birds had already developed protocols, identified target species, and provided preliminary data that would ensure we could complete this study successfully and with the maximum degree of application to forest management and bird species conservation.

We chose not to focus on other taxa such as small mammals or herptiles for two important reasons. First, as discussed above we believe forest birds are by far the best model for this study. Second, given the timeline, available budget, and nature of the study questions, we felt that we could do justice only to one group of species. Adding additional species groups to the study of avifauna would seriously have diluted our effort and compromised our ability to answer the study questions for forest birds.

1.2. Scientific Rationale

There are numerous reasons why measures of avian abundance (derived from point counts) and density (derived from spot mapping) may not be well correlated with the reproductive success of birds, and therefore, actual habitat quality. Of central importance is that point-count and spot-mapping methodologies rely heavily on the presence, location, and detection of singing males; females are essentially ignored (not necessarily intentionally, but because they are simply less vocal and conspicuous). Why would we expect an abundance of singing males to necessarily indicate greater habitat quality? There are at least three reasons why they might not:

(1) Dominant males that return to breeding grounds before subordinate males (Francis and Cooke 1986) are likely to occupy habitat in order of its quality (Marra et al. 1998). Such "high-status" males (alpha males) are able to establish and maintain large territories relative to the more common subordinates (beta males) who are forced into suboptimal habitat (Gauthreaux 1978 and references therein, Ekman and Askenmo 1984, Marra et al. 1998); territoriality and behavioral dominance hierarchies among males of a species may actually therefore limit the breeding density of birds in habitat of the highest quality (Krebs 1971). In this way, the relative abundance and/or density of males may actually be inversely correlated with habitat quality. Moreover, if beta males outnumber alpha males, then suboptimal habitats may contain higher densities of birds where song rates (and hence detectability) of males have been shown to be higher for some passerines (e.g., McShea and Rappole 1997). The importance of breeding early, and thereby increasing the likelihood that fledglings are recruited into the breeding population, also has been documented for some forest birds (Verboven and Visser 1998);

(2) Females, who typically arrive at breeding grounds after males (Francis and Cooke 1986), may preferentially mate with alpha males that occupy the "best" habitat, leaving beta males unmated well into the breeding season (if not for its duration). As a result, unmated beta males, who actually occupy poorer quality habitat (Krebs 1971), may sing more than mated alpha males as they constantly (perhaps desperately) attempt to attract females. Song output, and hence detectability by human observers, of paired males of many monogamous species is well known to be typically far below that of unpaired males (Best 1981, Gibbs and Faaborg 1990). One underlying assumption of point-count surveys is that all individuals present in survey populations have the same average probability of being detected (Caughley 1977); this assumption clearly has the potential to be violated and may lead to strongly biased abundance estimates and erroneous conclusions about patterns of habitat selection by breeding individuals (Gibbs and Faaborg 1990); and

(3) Males and females of a species behave very differently from one another: the former is more concerned with finding a prominent perch from which to advertise his territory and scan the neighborhood for potential intruding conspecifics (e.g., Sallabanks 1993); the latter is preoccupied with finding safe nesting cover in which to build a nest and raise a successful brood. This fundamental difference in behavioral ecology may have serious ramifications for research biologists that only sample singing males. In an ongoing study in Ontario, Lautenschlager (1997) has found that males and females show distinctly different habitat preferences and that those of the female are more strongly correlated with reproductive success.

1.3. Research Questions and Hypotheses

Our two-year research project addressed the following two questions:

(i) ***What are the relationships between relative avian abundance and density as derived from traditional point-count survey and spot-mapping techniques, respectively, and how do these parameters correlate with habitat quality as measured by reproductive success?*** Our null hypothesis was that avian abundance, density, and reproductive success are highly correlated across commonly occurring managed forest conditions.

(ii) ***Based upon meta-analyses of data collected in forest types of the southwest Cascade Mountains of Washington, as well as elsewhere in the PNW (east-central Washington, northeast Oregon, and west-central Idaho), for which species (or species' guilds) is relative abundance likely to be a misleading indicator of habitat quality?*** Our null hypothesis was that avian abundance and density are accurate measures of habitat quality throughout forests of the PNW.

1.4. Study Design

Our study was conducted in the Douglas-fir (*Pseudostuga menziesii*) - Western Hemlock (*Tsuga heterophylla*) zone (Franklin and Dyrness 1988) of the southwest Cascades of Washington. Data were collected in three principal forest types: (1) 8- to 12-year-old managed forest (regenerating clearcuts); (2) 40- to 60-year-old managed forest that had been commercially thinned, but not yet clear-cut harvested; and (3) 150- to 270-year-old mature, naturally regenerated old growth forest. Four replicates of each forest type were selected for study, spanning a variety of state, federal, and private ownerships (Table 1). Actual study plots were forest stands approximately 32

Table 1. Experimental design showing details of study plot treatment type, ownership, and name.

Forest Treatment	Ownership	Plot Name
8-12 year-old regenerating clearcut	Washington DNR	Gallup
	Washington DNR	Mineral
	Weyerhaeuser Company	Turner
	Champion Pacific Timberlands	O'Brian
40-60 year-old commercial thin	Washington DNR	Truck
	Weyerhaeuser Company	Johnson
	Weyerhaeuser Company	Deschutes
	Champion Pacific Timberlands	Five-O-One
150-270 year-old old growth	Washington DNR	Top Notch
	U.S. Forest Service	Nisqually
	U.S. Forest Service	Mona
	U.W. Pack Experimental Forest	Kirkland Pass

ha in size that matched these structural stage descriptions. We chose 32 ha because this was approximately equivalent to the maximum stand size available in our study area. While we would have preferred to work with larger plots (to increase sample points within stands), we could only work with what was available on the southwestern Washington Cascades landscape.

1.5. Criteria for Selecting Study Plots

One goal of our study was to make inferences for as much of the forest (in structural stages outlined in Table 1) within the Washington State Douglas-fir - Western Hemlock zone (e.g., the population) as possible. This would require that study plots be randomly selected from all potential plots that constituted that population. To achieve this, we identified a population of suitable study plots and randomly selected from among that population, as long as our sample did not create logistical bottlenecks for field staff that had to conduct surveys at all plots. We controlled for major factors that could influence within-stand bird population dynamics, such as the amount and type of disturbance in the immediate vicinity of the study plot (stand), size of study plot, and disturbance history of the study plot. We recognized that there also were potentially important influences of longitude, latitude, and elevation on the composition of bird communities in forests of the western Cascades (e.g., Huff and Raley 1991) and controlled for such factors during plot selection where possible. In January of 1998, we began identifying potential study plots by working with state resource agencies and private timber companies. All study plots were as homogeneous as possible with respect to forest structural stage (Table 1). Where necessary, we obtained permission from landowners to use privately owned land and were assured that the study plots would not be disturbed by forest management activities for at least two years.

2. Research Question #1a

What are the Relationships Between Relative Avian Abundance and Density as Derived from Traditional Point-count Survey and Spot-mapping Techniques, Respectively?

To answer this question, we collected field data that allowed us to estimate the following two parameters in all 12 study plots: (1) relative abundance using point counts; and (2) density using spot mapping. In addition, using our field data, we estimated a second measure of density using the software program DISTANCE (Buckland et al. 1993). DISTANCE software works on the premise that if distances to individual birds are recorded during point-count surveys, and other reasonable assumptions are met (Buckland et al. 1993), the shape of the relationship between distance and detectability can be modeled (detection probability functions), and estimates of absolute density reliably determined (Bibby et al. 2000). Detection probability functions derived separately for each species account for the fact that some species may be easier to detect in some habitat types (treatments) than others. We recognized the difficulty in measuring the distance to the origin of a vocal location; however, such distances are useful for determining detection curves as long as estimates are unbiased (i.e., random measurement error does not violate assumptions of the density estimation procedure; Buckland et al. 1993).

These measures of abundance and density were chosen because they represented community and population parameters typically studied, were recognized as nationally and internationally accepted standardized techniques, and allowed for the most thorough analysis of relationships between bird abundance and density. The following sections describe the specific protocols used and some general results in more detail.

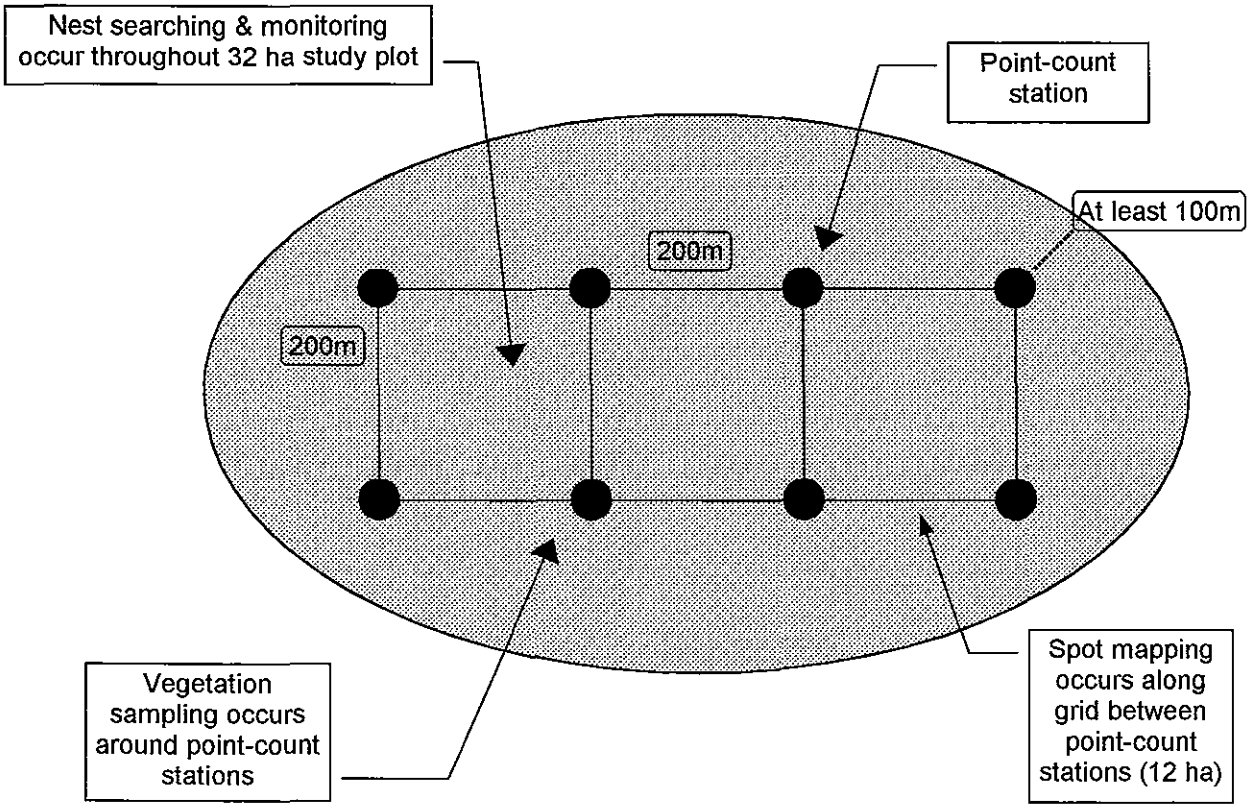
2.1.2. Measuring Relative Avian Abundance

2.1.1. ***Field protocols (point counts)*** - Relative breeding bird abundance was measured using standard point-count censusing techniques (Ralph et al. 1993), but with 10-min counts rather than 5-min counts. We recorded the time of each detection throughout the 10-min period to maintain data compatibility with other studies (e.g., Huff et al. 2000). Each study plot contained eight point-count stations arranged in a 2 x 4 grid wherever possible (Fig. 1). All count stations were 200 m apart, at least 100 m from plot boundaries, and centered within plot interiors whenever possible. All point-count locations were surveyed with a CMT MC-V hand-held GPS unit.

Each count station was visited five times during the period of April 27 through July 3, 1998 and April 21 through July 28, 1999. Counts were conducted between one half-hour after dawn and 0830 hr, and only on days free from inclement weather. All vocal and visual avian detections were identified to species and the distance between bird and observer estimated to the nearest meter for all birds within 100 m of observers. Distance was estimated using laser range finders. Birds recorded as being >100 m from observers were noted as such. Detections were considered to 100 m (rather than 50 m, as in most previous studies of songbirds in Washington) to maximize the effective area sampled within each forest stand. Sampling a larger area yielded more detections that would allow density estimates to be calculated for more species. Assumptions associated with using point counts are described in detail by Bibby et al. (2000). Ralph et al. (1995) provided a review of the use of point counts to monitor bird populations, but comparisons with demographic parameters (e.g., nest success or productivity) were not made. When point counting, birds flying above the canopy were recorded as such, and birds known to have been recorded at a previous point count within the plot were ignored. To minimize any bias in observer ability to detect and identify birds when conducting point counts (e.g., Cyr 1981, Bart and Schoultz 1984), observers rotated through stands on consecutive visits so that the same stand was never censused by the same individual more than once. Prior to collecting data, observers underwent intensive training to ensure that identification of birds in the field was as accurate as possible.

2.1.2. ***General results from point counts*** - Using these procedures, in 1998, we recorded 4,959 individual bird detections representing 59 species (excluding "flyovers"); in 1999, detections dropped to 4,470 birds representing 65 species (Table 2). Seven species were detected in 1998 that were not detected in 1999 (Cassin's Vireo, Golden-crowned Sparrow, Killdeer, Red-tailed Hawk, Great-horned Owl, Osprey, and Spotted Owl [scientific names in Table 2]). Thirteen species were detected in 1999 that were not detected in 1998 (Canada Goose, Red Crossbill, Chipping Sparrow, Downy Woodpecker, Northern Harrier, Belted Kingfisher, California Quail, Cooper's

Figure 1. Schematic diagram of overall sampling design for birds and habitat.



Hawk, Mourning Dove, Northern Goshawk, Sharp-shinned Hawk, Western Wood-pewee, and Yellow Warbler). These data combined bring the total number of birds detected during both years to 9,429 representing 72 species (Table 2).

Within 100 m of observers (i.e., limited distance counts), the same five species (e.g., Winter Wren, Chestnut-backed Chickadee, Pacific-slope Flycatcher, Dark-eyed Junco, and Song Sparrow) dominated the avian community in both years (Fig. 2). Winter Wrens consistently out-numbered other species by more than 200% and species relationships with forest treatment changed little between 1998 and 1999 (Fig. 2). The majority of proposed target species were well represented in the bird community. Due to the wide range of forest structural stages sampled, however, few species were well distributed among all three treatments. Winter Wrens, Pacific-slope Flycatchers, and Chestnut-backed Chickadees, the three most common bird species in our sample, all were more common in commercial thins and old growth forests

Table 2. Number of bird detections recorded during five visits to each of eight point count stations in all 12 study plots in the southwest Cascade Mountains of Washington, April–July, 1998 and 1999. Numbers are summarized by forest treatment and by birds detected within 100m of observers (limited distance counts) and all detections, regardless of distance from observers (unlimited distance counts); "flyovers" are excluded*. Species are listed in descending order of abundance, based upon total number of combined detections (i.e., unlimited distance counts summed between years).

			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
1	Winter Wren	1998	61	71	352	378	339	369	818
	Troglodytes troglodytes	1999	57	64	381	407	254	278	749
2	Pacific-slope Flycatcher	1998	20	23	199	207	146	148	378
	Empidonax difficilis	1999	13	17	82	88	111	116	221
3	Chestnut-backed Chickadee	1998	33	33	106	106	144	145	284
	Parus rufescens	1999	16	16	77	77	119	119	212
4	American Robin	1998	49	67	82	94	52	65	226
	Turdus migratorius	1999	82	97	86	120	27	38	255
5	Dark-eyed Junco	1998	128	128	121	121	18	18	267
	Junco oreganus hyemalis	1999	92	94	72	75	18	19	188
6	Song Sparrow	1998	224	234	6	6	1	1	241
	Melospiza melodia	1999	192	201	4	6	0	1	208
7	Varied Thrush	1998	12	42	28	49	82	129	220
	Ixoreus naevius	1999	29	42	44	58	96	127	227
8	Willow Flycatcher	1998	206	210	1	1	1	1	212
	Empidonax trailii	1999	172	186	1	1	0	0	187

			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
9	Hermit/Townsend's Warbler	1998	0	0	124	140	54	66	206
	D. occidentalis/townsendi	1999	4	6	88	95	57	61	162
10	Golden-crowned Kinglet	1998	5	5	66	66	116	117	188
	Regulus satrapa	1999	9	9	42	42	86	87	138
11	Swainson's Thrush	1998	51	70	33	51	4	10	131
	Catharus ustulatus	1999	97	113	26	35	22	26	174
12	Spotted Towhee	1998	141	146	6	6	5	5	157
	Pipilo maculatus	1999	109	114	13	14	3	3	131
13	Orange-crowned Warbler	1998	110	110	2	2	0	1	113
	Vermivora celata	1999	161	164	5	6	0	1	171
14	MacGillivray's Warbler	1998	165	167	12	12	0	0	179
	Oporornis tolmiei	1999	83	88	5	5	1	1	94
15	Brown Creeper	1998	1	3	32	32	64	67	102
	Certhia americana	1999	1	1	62	63	89	92	156
16	Steller's Jay	1998	24	50	18	25	30	44	119
	Cyanocitta stelleri	1999	20	51	13	29	27	40	120
17	Wilson's Warbler	1998	87	89	36	38	17	21	148
	Wilsonia pusilla	1999	40	44	27	29	18	18	91
18	Common Yellowthroat	1998	105	107	0	0	0	0	107
	Geothlypis trichas	1999	86	87	0	0	0	0	87
19	Red-breasted Nuthatch	1998	1	9	22	39	32	44	92
	Sitta canadensis	1999	2	6	10	19	48	62	87

			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
20	Gray Jay	1998	5	5	38	42	18	23	70
	Nucifraga columbiana	1999	4	6	35	39	22	26	71
21	Hairy Woodpecker	1998	13	16	26	28	20	24	68
	Picoides villosus	1999	9	13	28	31	17	23	67
22	Rufous Hummingbird	1998	43	43	5	5	4	4	52
	Selasphorus rufus	1999	69	69	7	7	6	6	82
23	Western Tanager	1998	8	11	48	59	7	8	78
	Piranga ludoviciana	1999	8	8	27	34	6	6	48
24	Northern Flicker	1998	17	28	2	13	8	11	52
	Colaptes auratus	1999	18	38	5	9	4	10	57
25	White-crowned Sparrow	1998	40	47	1	1	0	0	48
	Zonotrichia leucophrys	1999	27	38	6	7	1	2	47
26	Hutton's Vireo	1998	2	5	30	34	1	2	41
	Vireo huttoni	1999	9	15	21	22	5	6	43
27	Black-headed Grosbeak	1998	36	44	3	5	0	2	51
	Pheucticus melanocephalus	1999	22	25	1	1	2	2	28
28	Black-throated Gray Warbler	1998	0	0	27	33	4	4	37
	Dendroica nigrescens	1999	2	2	33	33	0	0	35
29	Warbling Vireo	1998	21	24	7	9	0	0	33
	Vireo gilvus	1999	18	21	4	5	0	0	26
30	Evening Grosbeak	1998	0	0	21	22	0	0	22
	Coccothraustes vespertina	1999	2	3	17	23	8	8	34

			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
31	Purple Finch	1998	4	4	14	16	0	0	20
	Carpodacus purpureus	1999	0	1	25	29	0	0	30
32	Band-tailed Pigeon	1998	3	3	4	7	5	14	24
	Columba fasciata	1999	0	4	2	2	16	18	24
33	Blue Grouse	1998	6	10	0	0	3	5	15
	Dendragapus obscurus	1999	15	21	1	1	4	10	32
34	Common Raven	1998	1	3	3	7	2	8	18
	Corvus corax	1999	1	3	6	13	0	3	19
35	Olive-sided Flycatcher	1998	8	15	0	0	0	0	15
	Contopus borealis	1999	11	16	0	0	2	2	18
36	American Goldfinch	1998	20	21	0	0	0	0	21
	Carduelis tristis	1999	10	11	0	0	0	0	11
37	Bewick's Wren	1998	8	8	3	3	0	0	11
	Thryomanes bewickii	1999	14	15	1	1	0	0	16
38	Pileated Woodpecker	1998	0	0	1	6	3	7	13
	Dryocopus pileatus	1999	0	1	3	6	4	7	14
39	American Crow	1998	0	1	2	3	0	0	4
	Corvus brachyrhynchos	1999	0	7	5	9	0	3	19
40	Hermit Thrush	1998	0	0	0	1	7	12	13
	Catharus guttatus	1999	7	7	0	0	1	1	8
41	Northern Pygmy-owl	1998	0	0	1	2	3	3	5
	Glaucidium gnoma	1999	0	0	1	1	8	11	12

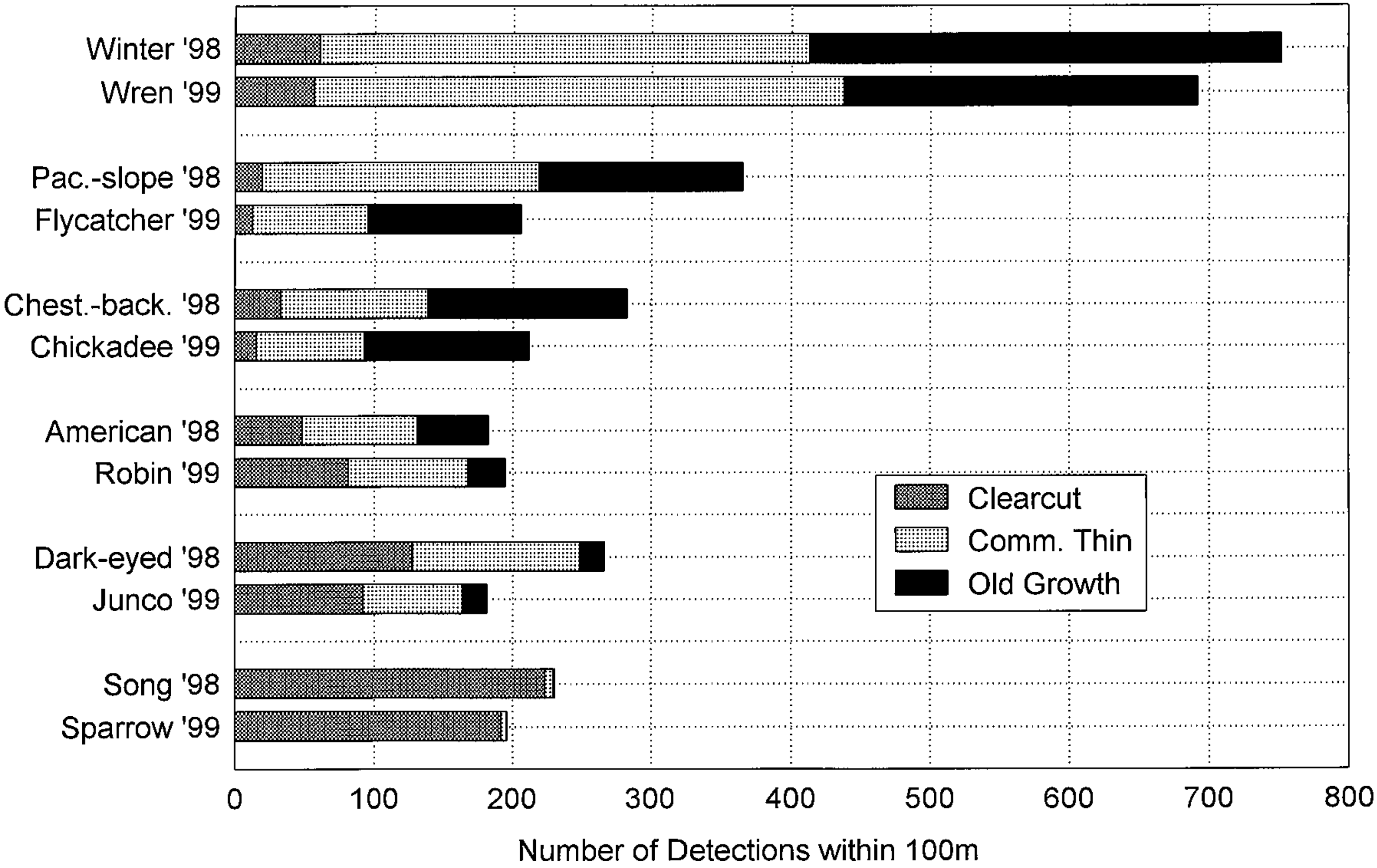
			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
42	Canada Goose	1998	0	0	0	0	0	0	0
	Branta canadensis	1999	0	3	2	4	0	8	15
43	Yellow-rumped Warbler	1998	8	8	1	1	2	2	11
	Dendroica coronata	1999	1	1	1	1	0	0	2
44	Cedar Waxwing	1998	7	7	2	2	0	0	9
	Bombycilla cedrorum	1999	3	3	0	0	0	0	3
45	Hammond's Flycatcher	1998	0	0	0	0	2	2	2
	Empidonax hammondii	1999	0	0	7	8	1	1	9
46	Red-breasted Sapsucker	1998	0	0	1	2	5	5	7
	Sphyrapicus nuchalis	1999	0	0	0	1	1	3	4
47	Ruby-crowned Kinglet	1998	1	1	0	0	0	0	1
	Regulus calendula	1999	7	8	0	0	0	0	8
48	Ruffed Grouse	1998	1	1	0	1	0	0	2
	Bonasa umbellus	1999	5	5	1	1	0	0	6
49	Black-capped Chickadee	1998	5	5	0	0	1	1	6
	Parus atricapillus	1999	1	1	0	0	0	0	1
50	Barred Owl	1998	0	0	0	1	1	2	3
	Strix varia	1999	0	0	0	0	1	1	1
51	Brown-headed Cowbird	1998	0	0	2	2	0	0	2
	Molothrus ater	1999	2	2	0	0	0	0	2
52	Pine Siskin	1998	2	2	0	0	0	0	2
	Carduelis pinus	1999	1	1	1	1	0	0	2

			Clearcut		Comm. Thin		Old Growth		Grand
No.	Bird Species	Year	≤100m	all	≤100m	all	≤100m	all	Total
53	Cassin's Vireo	1998	1	1	2	2	0	0	3
	Vireo cassinii	1999	0	0	0	0	0	0	0
54	Golden-crowned Sparrow	1998	3	3	0	0	0	0	3
	Zonotrichia atricapilla	1999	0	0	0	0	0	0	0
55	Red Crossbill	1998	0	0	0	0	0	0	0
	Loxia curvirostra	1999	0	0	0	0	3	3	3
56	Townsend's Solitaire	1998	1	2	0	0	0	0	2
	Myadestes townsendi	1999	0	0	1	1	0	0	1
57	Chipping Sparrow	1998	0	0	0	0	0	0	0
	Spizella passerina	1999	1	1	1	1	0	0	2
58	Downy Woodpecker	1998	0	0	0	0	0	0	0
	Picoides pubescens	1999	1	1	0	0	1	1	2
59	Killdeer	1998	0	2	0	0	0	0	2
	Charadrius vociferus	1999	0	0	0	0	0	0	0
60	Northern Harrier	1998	0	0	0	0	0	0	0
	Circus cyaneus	1999	2	2	0	0	0	0	2
61	Red-tailed Hawk	1998	0	1	0	0	0	1	2
	Buteo jamaicensis	1999	0	0	0	0	0	0	0
62	Belted Kingfisher	1998	0	0	0	0	0	0	0
	Ceryle alcyon	1999	0	1	0	0	0	0	1
63	California Quail	1998	0	0	0	0	0	0	0
	Callipepla californica	1999	1	1	0	0	0	0	1

No.	Bird Species	Year	Clearcut ≤100m	Clearcut all	Comm. Thin ≤100m	Comm. Thin all	Old Growth ≤100m	Old Growth all	Grand Total
64	Cooper's Hawk	1998	0	0	0	0	0	0	0
	Accipiter cooperi	1999	0	0	1	1	0	0	1
65	Great Horned Owl	1998	0	0	0	1	0	0	1
	Bubo virginianus	1999	0	0	0	0	0	0	0
66	Mourning Dove	1998	0	0	0	0	0	0	0
	Zenaida macroura	1999	0	0	0	0	0	1	1
67	Northern Goshawk	1998	0	0	0	0	0	0	0
	Accipiter gentilis	1999	0	0	0	0	0	1	1
68	Osprey	1998	0	0	0	0	0	1	1
	Pandion haliaetus	1999	0	0	0	0	0	0	0
69	Spotted Owl	1998	0	0	0	0	1	1	1
	Strix occidentalis	1999	0	0	0	0	0	0	0
70	Sharp-shinned Hawk	1998	0	0	0	0	0	0	0
	Accipiter striatus	1999	1	1	0	0	0	0	1
71	Western Wood-pewee	1998	0	0	0	0	0	0	0
	Contopus sordidulus	1999	0	0	0	0	1	1	1
72	Yellow Warbler	1998	0	0	0	0	0	0	0
	Dendroica petechia	1999	1	1	0	0	0	0	1

* The following species were detected only as "flyovers," and were excluded from analyses: Blue-winged Teal (*Anas discors*), Mallard (*Anas platyrhynchos*), Common Merganser (*Mergus merganser*), Common Snipe (*Gallinago gallinago*), Great-blue Heron (*Ardea herodias*), Tree Swallow (*Tachycineta bicolor*), Violet-green Swallow (*Tachycineta thalassina*), and Vaux's Swift (*Chaetura vauxi*).

Figure 2. Detection rates for the six most common bird species in forests of the southwest Cascade Mountains of Washington, 1998 and 1999.



compared with regenerating clearcuts (Fig. 2). Dark-eyed Juncos, on the other hand, were commonly detected in clearcuts and commercial thins, but not in old growth. The Song Sparrow was restricted almost exclusively to clearcuts. Patterns such as these continued throughout the entire bird community, with structural stage "generalists" being conspicuously absent (Table 2). Only the American Robin was relatively evenly distributed with respect to forest treatment (Fig. 2).

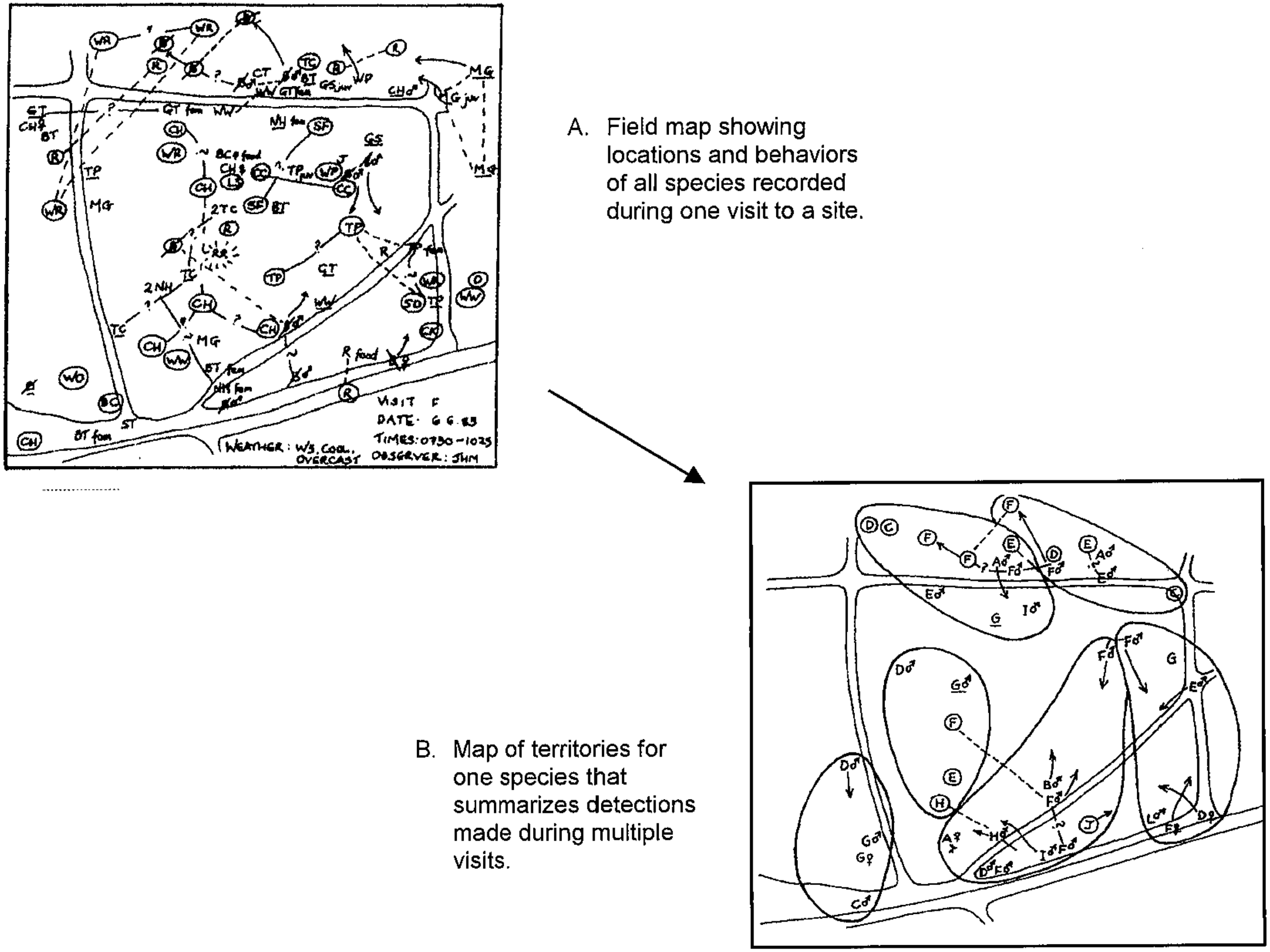
2.2. Measuring Bird Density

2.2.1. ***Field protocols (spot mapping)*** - Standardized spot-mapping techniques were used (IBCC 1969, 1970). Each study plot was visited 10 times during each of the 1998 and 1999 breeding season. In 1998, most mapping (nine visits) was conducted between one half-hour after dawn and 1030 hr, and only on days free from inclement weather. In addition, one evening visit was completed, but proved to be fruitless (i.e., relatively few bird detections were made); additional evening visits were therefore dropped. In 1999, all 10 visits were conducted during the early morning hours. Observers walked a grid established between point-count stations (Fig. 1) at a moderate speed (10–12 min/100 m), constantly recording the locations and territorial behaviors of all birds, and marking these locations on detailed maps of the spot-mapping plot (12 ha total area). We made frequent stops to check for simultaneous detections of the same species. All observations were marked on maps using standardized codes (Koskimies and Vaisanen 1991) and then transferred to species-specific maps. By mapping the locations of birds based upon territorial behavior we were able to count the number of territories in an area and thereby estimate the density of birds directly from field observations. Assumptions associated with using mapping techniques also are described in detail by Bibby et al. (2000).

2.2.2. ***General results from spot mapping*** - Ten visits per year to each of the 12 study plots resulted in an extensive data set of mapped species territories. Field maps were generated during each visit that contained records of all species (Fig. 3a). These were then converted into separate maps for individual species (Fig. 3b) according to the rules described by Bibby et al. (2000). Maps were prepared for at least five species (the most commonly detected ones) at each study plot for each of two years; for some plots, up to ten species were mapped.

2.2.3. ***Density estimates from DISTANCE software*** - One major problem with using relative bird abundance (as typically derived by point count surveys), as opposed to density, to test for effects of habitat quality is that detectability of species may vary by habitat type (e.g., old growth vs. thinned forests). Thus, differences in relative

Figure 3. Example of a field map generated during one spot-mapping session (A) and the resulting species-specific territory map that summarizes multiple spot-mapping visits to a site (B). Illustrations from Bibby et al. 2000.



A. Field map showing locations and behaviors of all species recorded during one visit to a site.

B. Map of territories for one species that summarizes detections made during multiple visits.

abundance attributed to habitat quality may, in fact, be related to differences in detectability. Estimates of density that account for detection probabilities, which may vary by treatment, are more appropriate for comparisons between treatments (Burnham et al. 1980). Traditionally, estimating density has been based on a finite population sampling approach (Cochran 1977). A typical finite sampling approach would consist of establishing a series of randomly distributed plots and then censusing the population within these plots. As an extension of this approach, distance sampling theory is based on the idea that individuals within plots may escape detection, and that there is a tendency for detectability to decrease with increasing distance from the observer. Program DISTANCE uses distances from the observer to the individual species to best fit a detection function (see Buckland et al. [1993] for a thorough description of distance sampling). The detection function defines the probability of detecting individuals as a function of distance from the observer. The expected density of a species in an area is equal to the number of individuals detected in that area, divided by the probability of detection for that area.

Buckland et al. (1993) suggest that fitting detection functions requires a sample size of at least 30 individuals per species. We fitted detection functions at the level of individual forest stands (when we had >29 detections of a species), and or at the forest treatment level (see Table 1) for all species with adequate sample sizes. We considered four detection model estimators (uniform with cosine adjustment, uniform with polynomial adjustments, half normal with hermite adjustment, and the hazard with cosine adjustment), and used Akaike's Information Criterion to select the best model. When we had detection functions at the stand and treatment levels resulting in two density estimates, we selected the density estimate with the lowest standard error for further analyses. In this way, density estimates using the program DISTANCE were calculated for 21 species (Appendix 1). We believe that other researchers would benefit greatly by designing their point-count studies to that program DISTANCE could be used in conjunction with more traditional methods of analyzing point-count data.

2.3. Calculating Abundance and Density, and Data Analysis

2.3.1. ***Relative avian abundance*** - For all species detected within 100 m of observers during point-count surveys, we computed mean detection rates per 10-min point count per forest stand sampled. We did this by pooling data among point-count stations within each stand (*n* = 8), among visits to each stand (*n* = 5), and between years (*n* = 2). Detection rates also were computed for three avian guilds (migratory, nesting, and feeding), as well as for all species combined, regardless of guild. Guild assignments followed those of Erhlich et al. (1988) and Sallabanks et al. (2001a) and are summarized in Appendix 2. Similar guild-level measures were computed for most other population parameters included in this report.

2.3.2. ***Abundance estimated at different point-count radii*** - To address relationships between abundance and density more fully, and to improve on our ability to assess past studies, we thought it useful to compare the relative accuracy of point-count data collected at different detection distances (point-count radii). In addition to the limited-distance estimates summarized above at 100-m point-count radii, therefore, we also calculated relative abundance of species and species' groups at 15-, 25-, 50-, and 75-m limited distance radii, as well as an unlimited distance count. We did this for as many species as we also had sufficient density and/or nest data to perform statistical comparisons (19 species and 10 species' guilds or groups).

2.3.3. ***Density from spot mapping*** - To generate unbiased estimates of territory numbers for as many species and study plots as possible, we employed one person, experienced with spot-mapping protocols, to examine all species' maps and use standardized procedures to delineate territories (see Fig. 3). As recommended by the International Bird Census Committee (IBCC 1969), edge clusters (i.e., partial territories that were mapped on the periphery of spot-mapping grids) were counted as being within the study plot if the majority of registrations for the cluster occurred within the grid. We chose to handle partial territories in this way (rather than combining all partial clusters with those wholly within the plot; e.g., Marchant 1983) to avoid overestimating the density of birds. Territory numbers per spot-mapping grid (12 ha) were then converted by species to numbers per ha per study plot for subsequent analyses. As with point count data, territory numbers were averaged between years. Such data yielded density estimates for 14 species and 10 species' guilds or groups. We chose not to further manipulate territory density (e.g., by doubling territory numbers to account for the presumed presence of females) when generating our measures of bird density. Our measures of density from spot-mapping data are perhaps therefore more accurately described as densities of male birds, since male birds comprise the majority of detections during spot mapping. The same is true, however, of both point-count data and estimates of density from DISTANCE. Hence, for consistency, we used unadjusted densities of territories (as calculated directly from field-generated maps) as measures of bird density.

2.3.4. ***Density from DISTANCE software*** - DISTANCE estimates of density (Appendix 1) were first averaged for each year (1998 and 1999) separately, then averaged between years to yield a mean number of birds per ha per two years for all species and all study plots (Table 3). With the exception of two species (Black-throated Gray Warbler and Hutton's Vireo) for which we lacked reliable data on relative abundance

Table 3. Mean density estimates for 1998–1999, and associated statistics, estimated using DISTANCE software for 21 bird species. For more details, such as year-specific values, see Appendix 1.

Bird Species	Forest Stand	Forest Treatment	Bird Density (No. / Ha)	Coefficent of Variation	Lower Confidence Limit	Upper Confidence Limit
American Robin	DESC	Comm Thin	0.44	0.06	0.19	0.99
	FIVE	Comm Thin	0.28	0.16	0.17	0.46
	GALL	Clearcut	0.50	0.60	0.00	557.81
	JOHN	Comm Thin	0.39	0.18	0.18	0.86
	KIRK	Old Growth	0.10	0.15	0.01	0.72
	MINE	Clearcut	0.10	0.13	0.02	0.48
	MONA	Old Growth	0.18	0.24	0.01	3.71
	NISQ	Old Growth	0.10	0.78	0.00	618.93
	OBRI	Clearcut	0.42	0.37	0.00	39.83
	TOPN	Old Growth	0.02	0.50	0.00	10.05
	TRUC	Comm Thin	0.10	0.40	0.00	13.13
	TURN	Clearcut	0.61	0.16	0.39	0.97
Brown Creeper	DESC	Comm Thin	0.28	0.69	0.00	755.39
	FIVE	Comm Thin	1.08	0.33	0.02	66.23
	JOHN	Comm Thin	0.40	0.33	0.10	1.63
	KIRK	Old Growth	1.35	0.35	0.46	3.97
	MONA	Old Growth	0.69	0.23	0.34	1.42
	NISQ	Old Growth	0.46	0.03	0.30	0.72
	TOPN	Old Growth	0.55	0.22	0.27	1.09
	TRUC	Comm Thin	0.36	0.17	0.25	0.50
Blk-td. G. Warb.	DESC	Comm Thin	0.64	0.10	0.53	0.79
	FIVE	Comm Thin	0.06	1.00	0.00	2170.60
	JOHN	Comm Thin	0.12	1.00	0.00	4883.90
	KIRK	Old Growth	0.05	1.00	0.00	2066.60
	TRUC	Comm Thin	0.00	0.00	0.00	0.00
Chst.-bd. Chick.	DESC	Comm Thin	1.23	0.26	0.05	31.30
	FIVE	Comm Thin	2.00	0.09	0.61	6.52
	GALL	Clearcut	1.20	0.10	0.97	1.47
	JOHN	Comm Thin	0.82	0.15	0.12	5.57
	KIRK	Old Growth	1.62	0.15	0.84	3.12
	MINE	Clearcut	0.62	0.72	0.00	2294.50
	MONA	Old Growth	2.35	0.19	1.03	5.40
	NISQ	Old Growth	1.59	0.17	0.77	3.30
	OBRI	Clearcut	0.10	1.00	0.00	3750.80
	TOPN	Old Growth	1.79	0.12	1.29	2.49
	TRUC	Comm Thin	1.89	0.33	0.03	119.14
	TURN	Clearcut	0.00	0.00	0.00	0.00
Com. Yellowtht.	GALL	Clearcut	0.00	0.00	0.00	0.00
	MINE	Clearcut	0.00	0.00	0.00	0.00
	OBRI	Clearcut	2.04	0.14	1.11	3.75
	TURN	Clearcut	5.36	0.21	0.41	70.74

Table 3. Mean density estimates for 1998–1999, and associated statistics, estimated using DISTANCE software for 21 bird species. For more details, such as year-specific values, see Appendix 1.

Bird Species	Forest Stand	Forest Treatment	Bird Density (No. / Ha)	Coefficent of Variation	Lower Confidence Limit	Upper Confidence Limit
Dark-eyed Jun.	DESC	Comm Thin	0.83	0.34	0.01	57.58
	FIVE	Comm Thin	0.20	0.61	0.00	239.20
	GALL	Clearcut	2.27	0.15	1.70	3.03
	JOHN	Comm Thin	1.81	0.19	0.79	4.12
	KIRK	Old Growth	0.16	0.40	0.00	21.27
	MINE	Clearcut	4.39	0.24	2.05	9.36
	MONA	Old Growth	0.08	0.00	0.08	0.08
	NISQ	Old Growth	0.23	0.52	0.00	109.64
	OBRI	Clearcut	1.34	0.17	0.64	2.81
	TOPN	Old Growth	0.03	0.60	0.00	32.36
	TRUC	Comm Thin	0.79	0.51	0.00	342.41
	TURN	Clearcut	0.59	0.52	0.00	300.84
Gold.-crd. King.	DESC	Comm Thin	2.30	0.17	1.54	3.45
	FIVE	Comm Thin	1.08	0.83	0.00	10477.00
	JOHN	Comm Thin	0.74	0.24	0.27	2.01
	KIRK	Old Growth	1.01	0.48	0.14	7.18
	MONA	Old Growth	1.68	0.14	1.23	2.29
	NISQ	Old Growth	2.02	0.23	0.75	5.44
	TOPN	Old Growth	2.25	0.09	1.86	2.72
	TRUC	Comm Thin	0.44	0.35	0.01	34.01
Hm/Town. Warb.	DESC	Comm Thin	0.70	0.23	0.27	1.86
	FIVE	Comm Thin	0.44	0.14	0.33	0.59
	JOHN	Comm Thin	0.69	0.16	0.47	1.01
	KIRK	Old Growth	0.36	0.12	0.27	0.47
	MONA	Old Growth	0.14	1.00	0.00	5407.80
	NISQ	Old Growth	0.39	0.10	0.32	0.47
	TOPN	Old Growth	0.07	0.57	0.00	58.98
	TRUC	Comm Thin	0.09	0.56	0.00	64.34
Hutton's Vireo	DESC	Comm Thin	0.25	0.45	0.00	59.12
	FIVE	Comm Thin	0.13	0.50	0.00	53.62
	JOHN	Comm Thin	0.03	0.20	0.00	0.36
	TRUC	Comm Thin	.10351E-01 1	0.00	0.00	406.57
MacGilly's Warb.	GALL	Clearcut	0.61	0.44	0.00	123.24
	MINE	Clearcut	0.83	0.24	0.04	17.28
	OBRI	Clearcut	1.37	0.41	0.01	210.99
	TURN	Clearcut	0.63	0.18	0.29	1.37
Org.-crnd. Warb.	GALL	Clearcut	1.39	0.27	0.05	42.90
	MINE	Clearcut	1.11	0.07	0.91	1.35
	OBRI	Clearcut	0.64	0.13	0.13	3.22
	TURN	Clearcut	1.71	0.32	0.03	93.16

Table 3. Mean density estimates for 1998–1999, and associated statistics, estimated using DISTANCE software for 21 bird species. For more details, such as year-specific values, see Appendix 1.

Bird Species	Forest Stand	Forest Treatment	Bird Density (No. / Ha)	Coefficent of Variation	Lower Confidence Limit	Upper Confidence Limit
Pacific-slope Fly.	DESC	Comm Thin	0.26	0.46	0.00	68.05
	FIVE	Comm Thin	1.55	0.44	0.01	309.79
	GALL	Clearcut	0.28	0.26	0.17	0.48
	JOHN	Comm Thin	0.92	0.48	0.00	296.27
	KIRK	Old Growth	1.27	0.25	0.05	30.71
	MINE	Clearcut	0.02	1.00	0.00	637.90
	MONA	Old Growth	1.38	0.13	0.80	2.38
	NISQ	Old Growth	0.99	0.21	0.07	14.50
	OBRI	Clearcut	0.02	1.00	0.00	964.72
	TOPN	Old Growth	0.33	0.19	0.15	0.74
	TRUC	Comm Thin	0.73	0.27	0.02	22.44
	TURN	Clearcut	0.00	0.00	0.00	0.00
Red-brsd. Nut.	DESC	Comm Thin	0.00	1.00	0.00	162.73
	FIVE	Comm Thin	0.07	0.64	0.00	112.88
	JOHN	Comm Thin	0.06	0.33	0.00	3.49
	KIRK	Old Growth	0.09	0.16	0.01	0.69
	MONA	Old Growth	0.25	0.46	0.00	68.11
	NISQ	Old Growth	0.03	1.00	0.00	1275.80
	TOPN	Old Growth	0.09	0.00	0.09	0.09
	TRUC	Comm Thin	0.07	0.38	0.00	8.03
Song Sparrow	GALL	Clearcut	1.07	0.16	0.15	7.79
	MINE	Clearcut	1.51	0.23	0.08	26.91
	OBRI	Clearcut	3.32	0.13	1.94	5.70
	TURN	Clearcut	4.45	0.07	3.81	5.18
Spotted Towhee	GALL	Clearcut	0.53	0.36	0.01	46.37
	MINE	Clearcut	1.00	0.09	0.81	1.24
	OBRI	Clearcut	1.17	0.07	1.03	1.33
	TURN	Clearcut	1.85	0.23	0.10	34.82
Swain. Thrush	DESC	Comm Thin	0.19	0.20	0.02	2.31
	FIVE	Comm Thin	0.13	0.22	0.09	0.21
	GALL	Clearcut	0.55	0.08	0.47	0.65
	JOHN	Comm Thin	0.03	0.33	0.00	1.82
	KIRK	Old Growth	0.07	0.80	0.00	538.03
	MINE	Clearcut	0.85	0.58	0.00	829.02
	MONA	Old Growth	0.10	0.33	0.04	0.28
	NISQ	Old Growth	2.21	1.00	0.00	86825.00
	OBRI	Clearcut	0.33	0.28	0.01	11.21
	TOPN	Old Growth	0.04	1.00	0.00	1389.20
	TRUC	Comm Thin	0.07	0.33	0.00	4.52
	TURN	Clearcut	0.39	0.17	0.19	0.81

Table 3. Mean density estimates for 1998–1999, and associated statistics, estimated using DISTANCE software for 21 bird species. For more details, such as year-specific values, see Appendix 1.

Bird Species	Forest Stand	Forest Treatment	Bird Density (No. / Ha)	Coefficent of Variation	Lower Confidence Limit	Upper Confidence Limit
Varied Thrush	DESC	Comm Thin	0.07	1.00	0.00	2686.20
	FIVE	Comm Thin	0.18	0.21	0.11	0.27
	GALL	Clearcut	0.08	0.69	0.00	229.35
	JOHN	Comm Thin	0.00	0.00	0.00	0.00
	KIRK	Old Growth	0.23	0.02	0.17	0.31
	MINE	Clearcut	0.15	0.25	0.01	3.41
	MONA	Old Growth	0.21	0.44	0.00	43.01
	NISQ	Old Growth	0.21	0.21	0.02	2.93
	OBRI	Clearcut	0.00	0.00	0.00	0.00
	TOPN	Old Growth	0.26	0.15	0.04	1.78
	TRUC	Comm Thin	0.16	0.06	0.08	0.32
	TURN	Clearcut	0.02	1.00	0.00	625.14
White-crd. Sp.	GALL	Clearcut	0.13	0.33	0.00	8.20
	MINE	Clearcut	0.11	0.08	0.04	0.28
	OBRI	Clearcut	0.19	0.08	0.07	0.56
	TURN	Clearcut	0.16	0.36	0.00	13.12
Willow Fly.	GALL	Clearcut	0.80	0.50	0.00	337.10
	MINE	Clearcut	1.47	0.10	1.19	1.82
	OBRI	Clearcut	2.66	0.14	2.00	3.54
	TURN	Clearcut	1.98	0.20	1.26	3.10
Wilson's Warb.	DESC	Comm Thin	0.63	0.40	0.12	3.30
	FIVE	Comm Thin	0.16	0.00	0.16	0.16
	GALL	Clearcut	0.26	0.29	0.01	9.27
	JOHN	Comm Thin	0.00	0.00	0.00	0.00
	KIRK	Old Growth	0.24	0.20	0.10	0.56
	MINE	Clearcut	0.54	0.55	0.00	375.42
	MONA	Old Growth	0.13	0.50	0.00	51.47
	NISQ	Old Growth	0.28	0.11	0.22	0.35
	OBRI	Clearcut	0.23	0.42	0.00	37.47
	TOPN	Old Growth	0.01	1.00	0.00	577.98
	TRUC	Comm Thin	0.08	0.23	0.00	1.46
	TURN	Clearcut	0.18	0.27	0.01	5.25
Winter Wren	DESC	Comm Thin	3.15	0.27	0.99	9.98
	FIVE	Comm Thin	3.98	0.02	3.08	5.12
	GALL	Clearcut	1.33	0.11	1.05	1.68
	JOHN	Comm Thin	2.73	0.03	1.80	4.15
	KIRK	Old Growth	1.75	0.07	1.51	2.02
	MINE	Clearcut	0.33	0.38	0.00	32.98
	MONA	Old Growth	2.46	0.03	1.75	3.46
	NISQ	Old Growth	2.35	0.18	0.26	21.55
	OBRI	Clearcut	0.03	0.09	0.02	0.04
	TOPN	Old Growth	1.27	0.10	0.35	4.60
	TRUC	Comm Thin	1.75	0.33	0.03	99.09
	TURN	Clearcut	0.00	0.00	0.00	0.00

and territory numbers (density derived from spot mapping), the means of 1998 and 1999 combined were then used in subsequent analyses.

2.3.5. ***Tests for normality and homoscedasticity*** - Prior to analysis, data were screened for deviations from normality using the Shapiro-Wilks' W test (Shapiro et al. 1968) and for variance homogeneity using Levene's test (Levene 1960). Because data transformations were largely unsuccessful at correcting nonnormality and heteroscedasticity, we used nonparametric tests where necessary. Use of nonparametric statistics that rely on comparisons of ranks (e.g., Spearman rank correlation analysis) rather than raw data values was especially appropriate for most analyses because of the nature of our study objectives (i.e., to determine if those forest stands with the highest abundance or density of birds were also the stands with the highest rates of reproduction). Data analyses were performed using Statistica version 5.1 for Windows (StatSoft, Inc. 1996) and SYSTAT version 8.0 (SPSS, Inc., 1998). These tests were conducted prior to all analyses presented in this report; to minimize redundancy, however, we do not discuss them in subsequent sections.

2.3.6. ***Alpha level, statistical power, and multiple comparisons*** - Low sample sizes and a corresponding lack of statistical power increase the likelihood of committing Type II errors (Steidl et al. 1997). In applied research, such as we report on here, Type II errors may be more costly than Type I errors (Schmiegelow et al. 1997, Steidl et al. 1997, Sallabanks et al. 2000a). For these reasons, therefore, throughout this report (unless otherwise stated [i.e., song-rate study, see section 5]) we used an alpha level of 0.10 when interpreting the results of statistical tests. Also to reduce the risk of committing Type II errors, Bonferoni inequality adjustments (Manly 1992) to $\alpha = 0.10$ for multiple comparisons were not made.

2.4. Results and Discussion

2.4.1. ***Correlation between abundance and density*** - Correlation analyses between measures of relative avian abundance at different point-count radii (15-, 25-, 50-, 75-, and 100-m and unlimited distance) were significantly positively correlated with density estimates from spot-mapping procedures for the majority of species and species' groups (Table 4). For each detection distance to birds, we report correlation coefficients and associated *P*-values for 14 species and 10 species' groups. In particular, point counts appeared to be very reliable indicators of density for species such as the Dark-eyed Junco, Orange-crowned Warbler, Song Sparrow, and Winter Wren (Table 4). Ground-nesting birds also has highly significant correlations between abundance and density, regardless of detection distance. Abundance and density

Table 4. Results from correlation analyses between relative avian abundance calculated for six different detection distances (point-count radii) and density estimates derived from spot mapping territories.

	Detection Distance to Birds (Point-count Radius)											
	15 m		25 m		50 m		75 m		100 m		Unlimited	
Species or Species' Group	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
American Robin	0.64	<0.10	0.45	0.22	0.61	<0.10	0.74	<0.05	0.80	<0.05	0.82	<0.01
Brown Creeper	-0.26	0.57	0.29	0.53	0.54	0.21	0.46	0.30	0.45	0.31	0.45	0.31
Chestnut-backed Chickadee	0.32	0.80	0.31	0.80	1.00	<0.001	0.71	0.50	0.65	0.55	0.65	0.55
Dark-eyed Junco[a]	0.90	<0.01	0.88	<0.01	0.98	<0.001	1.00	<0.001	0.99	<0.001	0.98	<0.001
Hermit/Townsend's Warbler	-0.91	<0.05	-0.40	0.50	0.56	0.32	0.57	0.31	0.55	0.34	0.66	0.23
MacGillivray's Warbler	0.96	<0.05	0.98	<0.05	0.98	<0.05	0.99	<0.05	0.99	<0.05	0.98	<0.05
Orange-crowned Warbler	0.95	<0.05	0.96	<0.05	0.98	<0.01	1.00	<0.001	0.99	<0.001	0.99	<0.01
Pacific-slope Flycatcher	0.32	0.43	0.78	<0.05	0.93	<0.01	0.93	<0.01	0.91	<0.01	0.89	<0.01
Song Sparrow[a]	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001
Spotted Towhee[a]	0.87	<0.01	0.92	<0.05	0.97	<0.01	0.97	<0.01	0.97	<0.01	0.97	<0.01
Varied Thrush	0.19	0.76	0.82	<0.10	0.65	0.23	0.61	0.27	0.70	0.19	0.70	0.19
Willow Flycatcher	0.76	0.24	0.86	0.14	0.97	<0.05	0.92	<0.10	0.89	0.11	0.89	0.11
Wilson's Warbler	1.00	<0.001	0.87	0.33	0.54	0.64	0.34	0.78	0.31	0.80	0.24	0.85
Winter Wren	0.74	<0.01	0.88	<0.001	0.92	<0.001	0.87	<0.001	0.85	<0.01	0.81	<0.01
Resident Birds	0.71	<0.05	0.75	<0.01	0.70	<0.05	0.61	<0.05	0.54	<0.10	0.34	0.27
Migrant Birds	0.79	<0.01	0.83	<0.01	0.83	<0.01	0.81	<0.01	0.79	<0.01	0.79	<0.01
Open-cup-Nesting Birds[a]	0.43	0.17	0.43	0.16	0.55	<0.10	0.59	<0.05	0.53	<0.10	0.60	<0.05
Ground-Nesting Birds[a]	0.88	<0.001	0.89	<0.001	0.88	<0.001	0.90	<0.001	0.90	<0.001	0.90	<0.001
Cavity-Nesting Birds	0.48	0.13	0.66	<0.05	0.58	<0.10	0.49	0.12	0.47	0.15	0.44	0.18
Foliage-Gleaning Birds[a]	0.43	0.16	0.66	<0.05	0.55	<0.10	0.59	<0.05	0.48	0.12	0.29	0.37
Ground-Feeding Birds	0.74	<0.05	0.78	<0.01	0.73	<0.05	0.70	<0.05	0.70	<0.05	0.63	<0.05
Bark-Gleaning Birds	0.41	0.36	0.65	0.12	0.53	0.22	0.49	0.27	0.51	0.25	0.48	0.27
Aerial-Feeding Birds	0.32	0.31	0.45	0.14	0.46	0.13	0.42	0.17	0.39	0.22	0.41	0.19
All Species Combined[a]	0.67	<0.05	0.69	<0.05	0.74	<0.01	0.73	<0.01	0.70	<0.05	0.55	<0.10

[a] Indicates correlation analyses performed using non-parametric Spearman rank correlation analysis due to nonnormal data. Otherwise, values of *r* are parametric Pearson product-moment correlation coefficients. Tests for normality were conducted using Shapiro-Wilks' W Test.

were not always correlated, however. Several species (e.g., Brown Creeper, Hermit/Townsend's Warbler, Varied Thrush) and some guilds (e.g., bark-gleaning and aerial-feeding birds) exhibited few or no correlations, perhaps because of the difficulty of accurately spot mapping the territories of these species or species' groups (Table 4). Results from these analyses are further summarized (Table 5).

Table 5. Summary of correlation analyses between relative avian abundance measured at different point-count radii and density derived from spot mapping. Numbers refer to the percentage of comparisons that were statistically significant, with *n* in parentheses.

	Detection Distance to Birds (Point-count Radius)					
Species' Group	15 m	25 m	50 m	75 m	100 m	Unlimited
Individual Species	64 (9)	57 (8)	71 (10)	64 (9)	57 (8)	57 (8)
Migratory Guilds	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)	50 (1)
Nesting Guilds	33 (1)	67 (2)	100 (3)	67 (2)	67 (2)	67 (2)
Feeding Guilds	25 (1)	50 (2)	50 (2)	50 (2)	25 (1)	25 (1)
All Species Combined	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)

Like density estimates derived from spot mapping, relative avian abundance was also significantly positively correlated with density estimates derived from DISTANCE software in the majority of cases (Table 6). For each detection distance to birds, we report correlation coefficients and associated *P*-values for 19 species and 10 species' groups. The high degree of correlation between point-count data and density derived from DISTANCE is likely due to the fact that the program DISTANCE generates estimates of density using relative abundance information. Strong positive correlations between the two measures are therefore expected. Despite this, two species (Swainson's Thrush and White-crowned Sparrow) were notable exceptions; for these species, relative abundance was uncorrelated with density at all point-count radii (Table 6). Results from these analyses are further summarized (Table 7).

2.4.2. *Comparison between the two measures of density* - We report mean values for both measures of density for 14 species and 10 species' groups in Table 8. To evaluate the effectiveness of using DISTANCE to compute bird density, we compared the two measures, assuming that spot mapping is a more accurate way to assess numbers of individuals per unit area. Species- and guild-specific correlation analyses suggest that, in approximately 50% of cases, the two measures of density are indeed

Table 6. Results from correlation analyses between relative avian abundance calculated for six different detection distances (point-count radii) and density estimates derived from DISTANCE software.

	Detection Distance to Birds (Point-count Radius)											
	15 m		25 m		50 m		75 m		100 m		Unlimited	
Species or Species' Group	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
American Robin	0.69	<0.05	0.78	<0.01	0.85	<0.001	0.81	<0.01	0.79	<0.01	0.74	<0.01
Brown Creeper	0.69	<0.10	0.96	<0.001	0.90	<0.01	0.94	<0.01	0.95	<0.001	0.95	<0.001
Chestnut-backed Chickadee	0.80	<0.01	0.87	<0.01	0.95	<0.001	0.96	<0.001	0.96	<0.001	0.96	<0.001
Common Yellowthroat	1.00	<0.10	1.00	<0.05	1.00	<0.01	1.00	<0.05	1.00	<0.001	1.00	<0.01
Dark-eyed Junco[a]	0.89	<0.001	0.93	<0.001	0.92	<0.001	0.94	<0.001	0.95	<0.001	0.96	<0.001
Golden-crowned Kinglet	0.86	<0.01	0.90	<0.01	0.91	<0.01	0.89	<0.01	0.88	<0.01	0.87	<0.01
Hermit/Townsend's Warbler	0.46	0.25	0.85	<0.01	0.99	<0.001	0.98	<0.001	0.98	<0.001	0.98	<0.001
MacGillivray's Warbler	0.34	0.66	0.84	0.17	0.99	<0.05	0.98	<0.01	1.00	<0.001	0.99	<0.01
Orange-crowned Warbler	0.89	0.11	0.89	0.11	0.97	<0.05	1.00	<0.01	1.00	<0.001	1.00	<0.01
Pacific-slope Flycatcher	0.75	<0.01	0.95	<0.001	0.97	<0.001	0.95	<0.001	0.95	<0.001	0.94	<0.001
Red-breasted Nuthatch[a]	0.58	0.13	0.33	0.43	0.93	<0.001	1.00	<0.001	0.99	<0.001	1.00	<0.001
Song Sparrow[a]	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001
Spotted Towhee[a]	0.80	0.20	0.95	<0.10	1.00	<0.001	1.00	<0.001	1.00	<0.001	1.00	<0.001
Swainson's Thrush	0.24	0.45	0.18	0.57	0.12	0.72	0.07	0.84	0.07	0.83	0.00	0.98
Varied Thrush	0.24	0.45	0.78	<0.01	0.97	<0.001	0.99	<0.001	0.98	<0.001	0.97	<0.001
White-crowned Sparrow[a]	0.00	1.00	0.40	0.60	0.40	0.60	0.74	0.26	0.60	0.40	0.60	0.40
Willow Flycatcher	0.97	<0.05	0.99	<0.05	0.96	<0.05	0.94	<0.10	0.92	<0.10	0.89	0.11
Wilson's Warbler	0.85	<0.001	0.83	<0.01	0.84	<0.01	0.74	<0.01	0.75	<0.01	0.75	<0.01
Winter Wren	0.93	<0.001	0.98	<0.001	0.98	<0.001	0.98	<0.001	0.98	<0.001	0.96	<0.001
Resident Birds	0.87	<0.001	0.83	<0.01	0.74	<0.01	0.70	<0.05	0.64	<0.05	0.41	0.19
Migrant Birds	0.94	<0.001	0.96	<0.001	0.96	<0.001	0.96	<0.001	0.95	<0.001	0.94	<0.001
Open-cup-Nesting Birds[a]	0.79	<0.001	0.79	<0.01	0.86	<0.01	0.87	<0.001	0.87	<0.01	0.85	<0.01
Ground-Nesting Birds[a]	0.90	<0.001	0.96	<0.001	0.91	<0.001	0.86	<0.001	0.85	<0.001	0.85	<0.001
Cavity-Nesting Birds	0.92	<0.001	0.94	<0.001	0.93	<0.001	0.94	<0.001	0.93	<0.001	0.92	<0.001
Foliage-Gleaning Birds[a]	0.74	<0.01	0.84	<0.01	0.87	<0.001	0.82	<0.01	0.76	<0.01	0.54	<0.10
Ground-Feeding Birds	0.76	<0.01	0.80	<0.01	0.66	<0.05	0.61	<0.05	0.59	<0.05	0.52	<0.10
Bark-Gleaning Birds	0.72	<0.05	0.80	<0.05	0.65	<0.10	0.74	<0.05	0.73	<0.05	0.69	<0.10
Aerial-Feeding Birds	0.27	0.39	0.49	0.11	0.62	<0.05	0.60	<0.05	0.57	<0.10	0.58	<0.10
All Species Combined[a]	0.74	<0.01	0.71	<0.05	0.71	<0.01	0.63	<0.05	0.62	<0.05	0.52	<0.10

[a] Indicates correlation analyses performed using non-parametric Spearman rank correlation analysis due to nonnormal data. Otherwise, values of *r* are parametric Pearson product-moment correlation coefficients. Tests for normality were conducted using Shapiro-Wilks' W Test.

Table 7. Summary of correlation analyses between relative avian abundance measured at different point-count radii and density derived from DISTANCE software. Numbers refer to the percentage of comparisons that were statistically significant, with *n* in parentheses.

	Detection Distance to Birds (Point-count Radius)					
Species' Group	15 m	25 m	50 m	75 m	100 m	Unlimited
Individual Species	69 (11)	74 (14)	89 (17)	89 (17)	89 (17)	84 (16)
Migratory Guilds	100 (2)	100 (2)	100 (2)	100 (2)	100 (2)	50 (1)
Nesting Guilds	100 (3)	100 (3)	100 (3)	100 (3)	100 (3)	100 (3)
Feeding Guilds	75 (3)	75 (3)	100 (4)	100 (4)	100 (4)	100 (4)
All Species Combined	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)	100 (1)

significantly correlated with each other (Table 8). That is, forest stands with the highest density of birds as determined by spot mapping also have the highest density of birds as determined using DISTANCE (and vice versa). In this sense, therefore, DISTANCE appeared reasonably accurate at measuring rank density. Measures of absolute density were less accurate, however. For most species and species' groups, density was overestimated using DISTANCE (Table 8). For several species (e.g., Orange-crowned Warbler, Song Sparrow, Spotted Towhee), the density of birds estimated using DISTANCE was more than double that estimated by spot mapping. Comparing the two measures on a plot-by-plot basis yielded many significant differences (Table 8). Of course, an alternative explanation is that spot mapping consistently underestimates density and that the higher DISTANCE estimates are the more realistic measure (D. Runde, *pers. comm.*).

As is suggested by a comparison between Tables 5 and 7, the correlation between relative abundance and density is greater for measures of density derived from DISTANCE compared with density determined by spot mapping (DISTANCE: mean ± SE $r = 0.84 \pm 0.02$; spot mapping: mean ± SE $r = 0.74 \pm 0.04$; Fig. 4). As discussed above, however, this may simply be due to the way DISTANCE uses abundance data to estimate density. Of greater interest is a comparison of how measures of relative abundance perform when calculated at different point-count radii. Regardless of which density measure one uses, the correlation with relative avian abundance sampled at small detection distances (i.e., 15- and 25-m point-count radii) tended to be low and highly variable (Fig. 4). Presumably, there are many birds that are not detected using such small point-count radii, perhaps because birds move away from the observer. Only when we examined detection distances of 50 m and greater did we find consistently high correlations between abundance and density. Importantly,

Table 8. Summary of density estimates derived from spot mapping (DENSPOT) and DISTANCE software (DENDIST) and results from comparative analyses between these measures for bird species and species' groups.

	Mean ± SE No. Birds / Ha (*N*)		Spearman Correlation[a]		Wilcoxon M-P Test[b]	
Species or Species' Group	DENSPOT	DENDIST	*r*	*P*	*Z*	*P*
American Robin	0.20 ± 0.02 (9)	0.27 ± 0.06 (12)	0.53	0.14	1.72	<0.10
Brown Creeper	0.32 ± 0.05 (7)	0.65 ± 0.13 (8)	0.41	0.36	2.37	<0.05
Chestnut-backed Chickadee	0.42 ± 0.13 (3)	1.38 ± 0.20 (11)	1.00	<0.0001	1.60	0.11
Dark-eyed Junco	0.56 ± 0.10 (9)	1.06 ± 0.37 (12)	0.92	<0.001	2.19	<0.05
Hermit/Townsend's Warbler	0.48 ± 0.05 (5)	0.36 ± 0.09 (8)	-0.15	0.80	0.13	0.89
MacGillivray's Warbler	0.54 ± 0.19 (4)	0.86 ± 0.18 (4)	0.87	0.33	1.60	0.11
Orange-crowned Warbler	0.53 ± 0.12 (5)	1.21 ± 0.23 (4)	1.00	<0.0001	1.83	<0.10
Pacific-slope Flycatcher	0.57 ± 0.07 (8)	0.70 ± 0.17 (11)	0.89	<0.01	2.24	<0.05
Song Sparrow	0.73 ± 0.31 (5)	2.59 ± 0.79 (4)	1.00	<0.0001	1.83	<0.10
Spotted Towhee	0.45 ± 0.06 (5)	1.14 ± 0.27 (4)	0.95	<0.10	1.83	<0.10
Varied Thrush	0.24 ± 0.03 (5)	0.13 ± 0.03 (12)	0.56	0.32	1.75	<0.10
Willow Flycatcher	0.79 ± 0.13 (4)	1.73 ± 0.39 (4)	0.80	0.20	1.83	<0.10
Wilson's Warbler	0.33 ± 0.07 (3)	0.23 ± 0.06 (12)	1.00	<0.0001	1.07	0.29
Winter Wren	1.36 ± 0.24 (11)	1.92 ± 0.35 (11)	0.87	<0.001	2.40	<0.05
Resident Birds	0.58 ± 0.05 (12)	0.84 ± 0.05 (12)	0.76	<0.01	2.82	<0.01
Migrant Birds	0.57 ± 0.08 (12)	0.72 ± 0.16 (12)	0.55	<0.10	1.41	0.16
Open-cup-Nesting Birds	0.45 ± 0.06 (12)	0.66 ± 0.10 (12)	0.48	0.12	2.59	<0.01
Ground-Nesting Birds	0.53 ± 0.09 (10)	0.90 ± 0.25 (12)	0.87	<0.01	2.40	<0.05
Cavity-Nesting Birds	0.89 ± 0.14 (11)	1.04 ± 0.14 (11)	0.43	0.12	1.24	0.21
Foliage-Gleaning Birds	0.72 ± 0.09 (12)	0.95 ± 0.09 (12)	0.50	0.10	1.87	<0.10
Ground-Feeding Birds	0.38 ± 0.07 (11)	0.66 ± 0.19 (12)	0.90	<0.001	1.87	<0.10
Bark-Gleaning Birds	0.30 ± 0.07 (12)	0.36 ± 0.07 (8)	0.44	0.32	0.51	0.61
Aerial-Feeding Birds	0.64 ± 0.07 (12)	1.00 ± 0.15 (12)	0.87	<0.001	2.82	<0.01
All Species Combined	0.60 ± 0.05 (12)	0.84 ± 0.07 (12)	0.62	<0.05	2.90	<0.01

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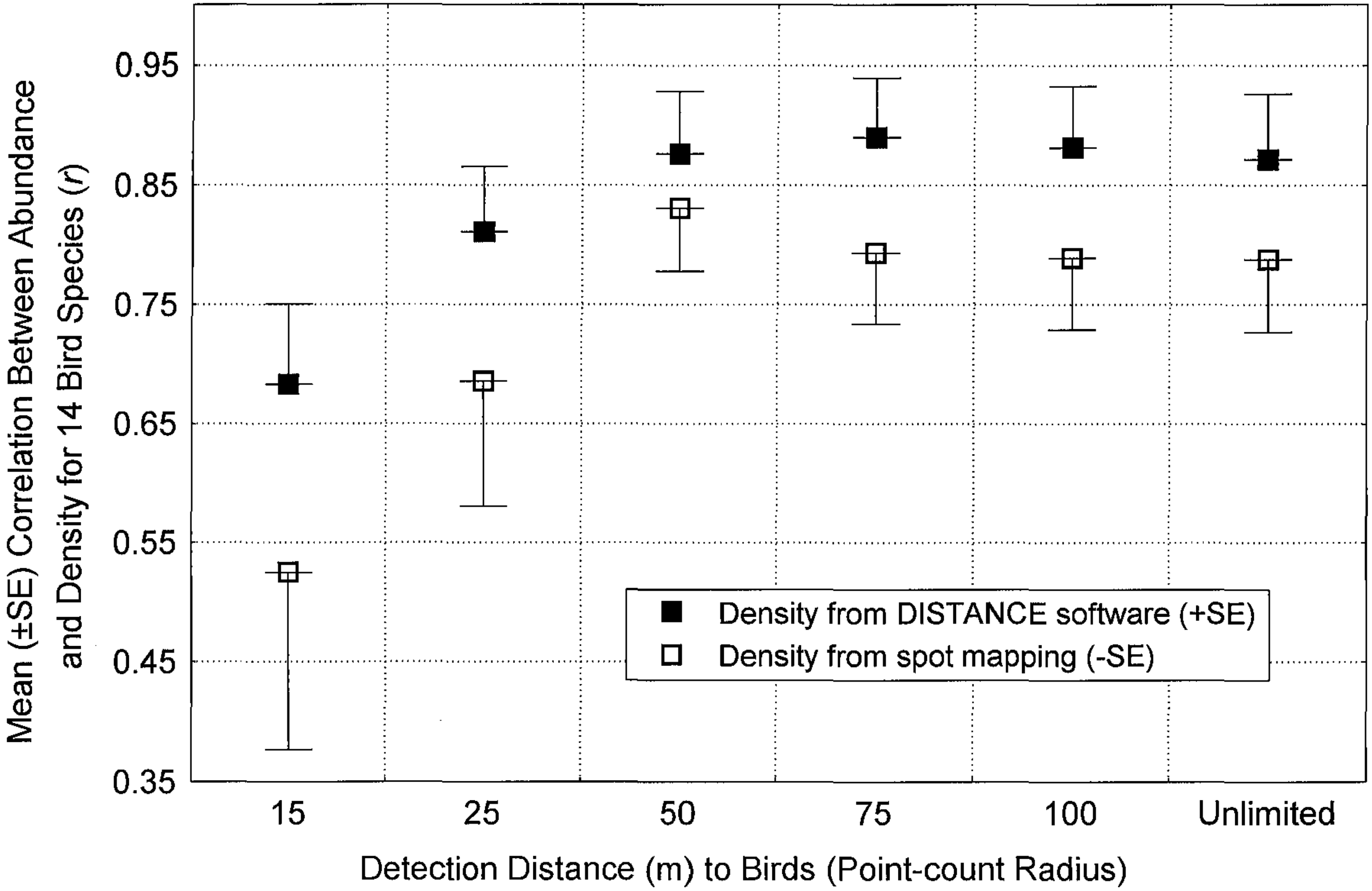
[a] Spearman rank correlation analysis performed on site-level density data for each species and species' group (minimum sample size of *n* = 3 required).

[b] Wilcoxon matched pairs test (with pair-wise deletion of missing data) used to compare density estimates at each study site for each species and species' group (minimum sample size of *n* = 3 required).

Figure 4. Comparison of correlations between relative avian abundance calculated at different point-count radii and two measures of density.



our results support using 50-m radius point-count surveys, a common distance that has become incorporated into most standardized point-count survey protocols (e.g., Ralph et al. 1993, 1995; Huff et al. 2000). Correlation coefficients between abundance and density determined by spot mapping were not significantly different among the six detection distances tested, most likely due to the high degree of within-groups variation for these data (Kruskal-Wallis ANOVA $H = 4.03$, df = 5, $n = 84$, $P = 0.54$; Kruskal and Wallis 1952). Correlation coefficients between abundance and density derived from DISTANCE were different among the six detection distances tested, however ($H = 14.88$, df = 5, $n = 114$, $P < 0.05$).

The Timber/Fish/Wildlife program has funded two major wildlife studies in Washington State: one that addressed the effects of forest stand age and fragmentation on wildlife ("Managed Forest study"; Aubry et al. 1997), and the second that addressed wildlife use of forested riparian management zones of different widths ("RMZ study"; O'Connell et al. 2000). While the Managed Forest study used standard point-count methods (with 50- and 75-m radius point counts on the Westside and Eastside, respectively), the RMZ study employed small point-count plots (10, 15 m fixed-radius point count plots/replicate) in western Washington and thin transects (modified belt transects of 30 x 800 m/replicate) in eastern Washington to sample narrow strips of riparian forest. Birds within transects were counted as a surveyor moved slowly down the center of the belt. The Westside study included nest monitoring but small sample sizes precluded the use of nest success as a measure of habitat quality (S.F. Pearson, *pers. comm.*). In addition to small radii survey plots, the survey area per replicate (forest stand) in the western and eastern portions of the RMZ study were relatively small, 0.7 and 2.4 ha, respectively, compared to survey areas of other studies in the Pacific Northwest (>12.3 ha, Carey et al. 1991; 21.2 ha, Gilbert and Allwine 1991; 21.2 ha, Manuwal 1991; 21.2 ha, Huff et al. 1991; 21.2 ha, Lundquist and Mariani 1991; 9.4 ha for western Washington, Aubry et al. 1997) and from 2.3–9.4 ha for eastern Washington, Hallett and O'Connell 1997; and 25.1 ha, this study).

Our data (summarized in Fig. 4) suggested that abundance determined from small radii (≤25 m) point counts had lower correlations with density than abundance determined from larger radii (≥50 m) point counts for some species. Furthermore, correlation coefficients between density and relative abundance for all birds combined tended to decrease with decreasing point-count radii below 50 m. Small point-count radii are problematic because some birds move away from the observer and/or because there is greater sampling error associated with relatively small survey areas. If birds are avoiding people, then counting birds along a transect may exacerbate the problem since a moving observer likely frightens birds more than a stationary observer. If, on the other hand, sampling error associated with small areas is the main problem, then narrow transects are not an inherently inappropriate sampling technique.

Transects need only be large enough to minimize sampling error associated with small survey areas.

The RMZ study may have suffered from both types of sampling problems: small sample radii and small sample areas per replicate. These problems, in combination with our results (summarized in Table 6), suggest that the RMZ study may have produced unreliable abundance estimates for the American Robin, Brown Creeper, Hermit/Townsend's Warbler, MacGillivray's warbler, Red-Breasted Nuthatch, Swainson's Thrush, Varied Thrush, and White-crowned Sparrow, and aerial feeders as a group. Importantly, the RMZ study concluded that the abundance of the American Robin, White-crowned Sparrow, and Pacific-slope Flycatcher (an aerial feeder) were significantly different among treatments in western Washington and that the abundance of Red-breasted Nuthatches was significantly different among treatments in eastern Washington (O'Connell et al. 2000). If observer movement increases avoidance behavior in birds, then some results of the eastern portion of the RMZ study may be particularly suspect. Clearly, using consistent methods across treatments, as was the case in both the east and west portion of the RMZ study, will help minimize the effect of these sampling problems. Nonetheless, it seems unlikely that the RMZ study sampling protocols provided an index of abundance, that is, a measure that was correlated with true abundance for some species.

We suggest that results from forest studies using small radii point counts (including narrow transects) and small survey areas be used cautiously, especially for species (listed above) whose relative abundance at small detection radii is poorly correlated with density. If other measures of habitat quality (e.g., nest success, territory mapping) cannot be employed, bird surveys should include counts of birds that move away from an observer. One critical assumption of program DISTANCE is that the probability of detection is 1.0 at zero distance from a point-count station (Buckland et al. 1993). In other words, it is important to observe the location of birds as if they were undisturbed by the observer. This recommendation is in contrast to the idea that observers should wait several minutes at a station to allow birds to "settle" before beginning a point count. Perhaps a settling period allows birds to move back into an area after initially moving away in response to the observer? However, to our knowledge, no one has tested this idea in forests of the Pacific Northwest.

3. Research Question #1b

How Do Relative Avian Abundance and Density Correlate with Habitat Quality as Measured by Avian Reproductive Success?

To answer this question, we collected additional field data that allowed us to estimate reproductive effort of birds in all 12 study plots. Nest monitoring was chosen as the preferred method by which to measure reproductive success because it would yield the most accurate data on reproductive output and rates of nest predation. There are other recently developed techniques that also could have been used to evaluate the relationship between habitat quality and reproductive success (e.g., behavior mapping). However, while such techniques may carry some advantages over spot mapping, nest monitoring remained the best method for addressing habitat quality-reproductive success relationships (Vickery et al. 1992b). We assumed that true habitat quality was most accurately reflected by net reproductive output of birds (i.e., number of offspring successfully fledged). Others who have studied non-breeding birds have used other measures, such as Corticosterone levels, as indicators of habitat quality (Marra and Holberton 1998).

3.1. Measuring Avian Reproductive Success

3.1.1. ***Field protocols (nest searching and monitoring)*** - Standardized techniques were used to search for and monitor nests (Martin and Geupel 1993) in all 12 32-ha study plots during each songbird-nesting season. All nests found were monitored every three to four days and their fate recorded (i.e., successful, deserted, preyed upon, parasitized by cowbirds, or fate unknown). A nest was considered "successful" if it successfully fledged at least one host young. All nests were checked on days when nestlings were predicted to fledge (fledglings usually stayed nearby nests for a few days) in order to remove uncertainty as to whether they did indeed fledge. Types of nest predators (e.g., whether avian, mammalian, or reptilian) were identified where possible. Vegetative characteristics associated with all nests were measured following the national Breeding BIology Research and monitoring Database (BBIRD) protocols (Martin and Conway 1994), with a few modifications. All nest locations were mapped within the spot-mapping grid.

Nests of five to 10 target species (e.g., Pacific-slope Flycatcher, Winter Wren, Wilson's Warbler, Swainson's Thrush, Hutton's Vireo, American Robin, Song Sparrow, and Dark-eyed Junco) were the focus of nest searching efforts, although every nest found, regardless of species, was monitored. These target species were either the same as, or had ecologically similar counterparts to, those also targeted for ongoing studies elsewhere in the PNW (e.g., Sallabanks 1995, Sallabanks et al. 1999). When nest searching, every attempt was made to minimize predation events resulting from observers monitoring nests (as is known to happen from studies by Picozzi 1975, Bart 1978, Westmoreland and Best 1985, and Major 1989). Nests were approached from different directions on each visit and nests were not checked if corvids (i.e., Gray Jay, Steller's Jay, or Common Raven) and/or the Brown-headed Cowbird were present in the immediate area (increased predation by avian predators is the main reason for reduced nesting success of birds disturbed by observers; Götmark 1992). At critical points in the nesting cycle (e.g., hatching), adult birds were flushed from nests to determine expected fledging dates. At other times (e.g., during incubation), it was often only necessary to ascertain whether a nest was still active by the presence of an incubating/feeding adult; this was always determined from as far away from the nest as possible. Careful nest monitoring techniques such as these (see also Ralph et al. 1993) have been shown to effectively reduce the probability that visited nests are more likely to be depredated than control nests (Willis 1973, Gottfried and Thompson 1978).

3.1.2. *General results from nest searching and monitoring* - We found and monitored 320 nests of 32 bird species in 1998 and 361 nests of 35 species in 1999; pooling data between years, we found and monitored 681 nests of 40 bird species (Table 9). Nest numbers were highly reflective of bird community composition, with more nests being found for the Winter Wren (n = 174) than any other bird species (again, Winter Wren nests out-numbered other species by more than 200%) (Table 9). As with abundance and density estimates, there also were few species for which we found nests well represented among all three forest treatments.

Pooling nest data between years, overall nest success was typical of other forest songbird studies (R. Sallabanks, *unpubl. data*), with >60% of all nests fledging young (Fig. 5), although there was considerable variation among species. For example, whereas the Dark-eyed Junco appeared to be a relatively successful nester among all treatments (78% of nests successful, on average), the American Robin suffered considerable nest failure rates (33% of nests successful, on average) (Table 9). Although the reasons remain obscure, birds nesting in clearcuts appeared to have the highest rates of nest success (66%) (Fig. 5). Among all treatments, the most common reason for nest failure was predation, although birds nesting in old growth forest appeared to abandon nests more often compared with other treatments (Fig. 6).

3.2. Calculating Reproductive Success and Data Analysis

3.2.1. *Measures of avian reproductive success* - To address the principle objective of our study, we calculated three measures of avian reproductive success for as many

Table 9. Nest numbers and nest fates for 40 species of forest birds studied in the southwest Cascade Mountains of Washington, April–August, 1998 and 1999. Data are pooled between years and are summarized by forest treatment. Species are listed in descending order of nest number, based upon combined totals. Scientific names are in Table 2.

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
1	Winter Wren	Successful	2	(2)	71	(71)	27	(27)	100	(57)
		Failed	1	(1)	48	(68)	22	(31)	71	(41)
		Unknown	0	(0)	2	(67)	1	(33)	3	(2)
		Treatment Totals	3	(2)	121	(70)	50	(29)	174	
2	Dark-eyed Junco	Successful	19	(31)	35	(56)	8	(13)	62	(78)
		Failed	4	(22)	12	(67)	2	(11)	18	(23)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	23	(29)	47	(59)	10	(13)	80	
3	Song Sparrow	Successful	44	(98)	1	(2)	0	(0)	45	(74)
		Failed	14	(88)	2	(13)	0	(0)	16	(26)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	58	(95)	3	(5)	0	(0)	61	
4	American Robin	Successful	6	(38)	9	(56)	1	(6)	16	(33)
		Failed	14	(48)	12	(41)	3	(10)	29	(60)
		Unknown	1	(33)	2	(67)	0	(0)	3	(6)
		Treatment Totals	21	(44)	23	(48)	4	(8)	48	
5	Pacific-slope Flycat.	Successful	0	(0)	13	(65)	7	(35)	20	(50)
		Failed	1	(5)	9	(45)	10	(50)	20	(50)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	1	(3)	22	(55)	17	(43)	40	

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
6	Chestnut-back. Chick.	Successful	0	(0)	10	(63)	6	(38)	16	(48)
		Failed	1	(20)	1	(20)	3	(60)	5	(15)
		Unknown	0	(0)	6	(50	6	(50)	12	(36)
		Treatment Totals	1	(3)	17	(36)	15	(45)	33	
7	Rufous Hummingbird	Successful	8	(44)	6	(33)	4	(22)	18	(56)
		Failed	1	(8)	9	(75)	2	(17)	12	(38)
		Unknown	0	(0)	0	(0)	2	(100)	2	(6)
		Treatment Totals	9	(28)	15	(47)	8	(25)	32	
8	Brown Creeper	Successful	0	(0)	5	(24)	16	(76)	21	(68)
		Failed	0	(0)	3	(75)	1	(25)	4	(13)
		Unknown	0	(0)	3	(50)	3	(50)	6	(19)
		Treatment Totals	0	(0)	11	(35)	20	(65)	31	
9	Common Yellowthroat	Successful	16	(100)	0	(0)	0	(0)	16	(70)
		Failed	6	(100)	0	(0)	0	(0)	6	(26)
		Unknown	1	(100)	0	(0)	0	(0)	1	(4)
		Treatment Totals	23	(100)	0	(0)	0	(0)	23	
10	Varied Thrush	Successful	1	(13)	1	(13)	6	(75)	8	(42)
		Failed	0	(0)	1	(17)	5	(83)	6	(32)
		Unknown	0	(0)	0	(0)	5	(100)	5	(26)
		Treatment Totals	1	(5)	2	(11)	16	(84)	19	
11	Willow Flycatcher	Successful	11	(100)	0	(0)	0	(0)	11	(73)
		Failed	4	(100)	0	(0)	0	(0)	4	(27)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	15	(100)	0	(0)	0	(0)	15	

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
12	Cedar Waxwing	Successful	8	(100)	0	(0)	0	(0)	8	(62)
		Failed	5	(100)	0	(0)	0	(0)	5	(38)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	13	(100)	0	(0)	0	(0)	13	
13	Hairy Woodpecker	Successful	3	(25)	3	(25)	6	(50)	12	(92)
		Failed	0	(0)	1	(100)	0	(0)	1	(8)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	3	(23)	4	(31)	6	(46)	13	
14	Spotted Towhee	Successful	5	(100)	0	(0)	0	(0)	5	(42)
		Failed	6	(86)	1	(14)	0	(0)	7	(58)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	11	(92)	1	(8)	0	(0)	12	
15	Red-breasted Nuthatch	Successful	0	(0)	4	(44)	5	(56)	9	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	4	(44)	5	(56)	9	
16	Swainson's Thrush	Successful	1	(17)	3	(50)	2	(33)	6	(67)
		Failed	1	(33)	2	(67)	0	(0)	3	(33)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	2	(22)	5	(56)	2	(22)	9	
17	Orange-crown. Warbler	Successful	2	(67)	1	(33)	0	(0)	3	(43)
		Failed	3	(75)	1	(25)	0	(0)	4	(57)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	5	(71)	2	(29)	0	(0)	7	

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
18	Black-headed Grosbeak	Successful	2	(100)	0	(0)	0	(0)	2	(33)
		Failed	4	(100)	0	(0)	0	(0)	4	(67)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	6	(100)	0	(0)	0	(0)	6	
19	Wilson's Warbler	Successful	1	(33)	2	(67)	0	(0)	3	(50)
		Failed	0	(0)	1	(33)	2	(67)	3	(50)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	1	(17)	3	(50)	2	(33)	6	
20	MacGillivray's Warbl.	Successful	2	(67)	1	(33)	0	(0)	3	(60)
		Failed	1	(50)	1	(50)	0	(0)	2	(40)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	3	(60)	2	(40)	0	(0)	5	
21	Northern Flicker	Successful	1	(33)	1	(33)	1	(33)	3	(75)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	1	(100)	0	(0)	1	(25)
		Treatment Totals	1	(25)	2	(50)	1	(25)	4	
22	Steller's Jay	Successful	3	(100)	0	(0)	0	(0)	3	(75)
		Failed	1	(100)	0	(0)	0	(0)	1	(25)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	4	(100)	0	(0)	0	(0)	4	
23	Warbling Vireo	Successful	1	(100)	0	(0)	0	(0)	1	(25)
		Failed	3	(100)	0	(0)	0	(0)	3	(75)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	4	(100)	0	(0)	0	(0)	4	

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
24	White-crowned Sparrow	Successful	4	(100)	0	(0)	0	(0)	4	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	4	(100)	0	(0)	0	(0)	4	
25	Bewick's Wren	Successful	1	(100)	0	(0)	0	(0)	1	(33)
		Failed	2	(100)	0	(0)	0	(0)	2	(67)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	3	(100)	0	(0)	0	(0)	3	
26	Northern Pygmy-owl	Successful	0	(0)	0	(0)	1	(100)	1	(33)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	1	(50)	1	(50)	2	(67)
		Treatment Totals	0	(0)	1	(33)	2	(67)	3	
27	Pileated Woodpecker	Successful	0	(0)	2	(67)	1	(33)	3	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	2	(67)	1	(33)	3	
28	Western Tanager	Successful	0	(0)	2	(100)	0	(0)	2	(67)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	1	(100)	0	(0)	1	(33)
		Treatment Totals	0	(0)	3	(100)	0	(0)	3	
29	American Goldfinch	Successful	1	(100)	0	(0)	0	(0)	1	(50)
		Failed	1	(100)	0	(0)	0	(0)	1	(50)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	2	(100)	0	(0)	0	(0)	2	

			Number (% in parentheses) of Nests						Nest Fate	
No.	Bird Species	Nest Fate	Clearcut		Comm. Thin		Old Growth		Totals	
30	Blue Grouse	Successful	2	(100)	0	(0)	0	(0)	2	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	2	(100)	0	(0)	0	(0)	2	
31	Common Raven	Successful	0	(0)	1	(50)	1	(50)	2	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	1	(50)	1	(50)	2	
32	Gray Jay	Successful	1	(50)	1	(50)	0	(0)	2	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	1	(50)	1	(50)	0	(0)	2	
33	Red-breast. Sapsucker	Successful	0	(0)	0	(0)	2	(100)	2	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	0	(0)	2	(100)	2	
34	Common Nighthawk	Successful	0	(0)	0	(0)	0	(0)	0	(0)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	1	(100)	1	(100)
		Treatment Totals	0	(0)	0	(0)	1	(100)	1	
35	Downy Woodpecker	Successful	0	(0)	0	(0)	1	(100)	1	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	0	(0)	1	(100)	1	

No.	Bird Species	Nest Fate	Number (% in parentheses) of Nests						Nest Fate	
			Clearcut		Comm. Thin		Old Growth		Totals	
36	Evening Grosbeak	Successful	0	(0)	0	(0)	0	(0)	0	(0)
		Failed	0	(0)	1	(100)	0	(0)	1	(100)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	1	(100)	0	(0)	1	
37	Golden-crown. Kinglet	Successful	0	(0)	1	(100)	0	(0)	1	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	1	(100)	0	(0)	1	
38	Hermit/Towns. Warbler	Successful	0	(0)	1	(100)	0	(0)	1	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	1	(100)	0	(0)	1	
39	Ruffed Grouse	Successful	0	(0)	1	(100)	0	(0)	1	(100)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	0	(0)	0	(0)
		Treatment Totals	0	(0)	1	(100)	0	(0)	1	
40	Spotted Owl	Successful	0	(0)	0	(0)	0	(0)	0	(0)
		Failed	0	(0)	0	(0)	0	(0)	0	(0)
		Unknown	0	(0)	0	(0)	1	(100)	1	(100)
		Treatment Totals	0	(0)	0	(0)	1	(100)	1	

Figure 5. Summary of nest fate, by forest treatment and for all treatments combined, for 681 nests of 40 forest bird species monitored in the southwestern Washington Cascades, 1998–1999.

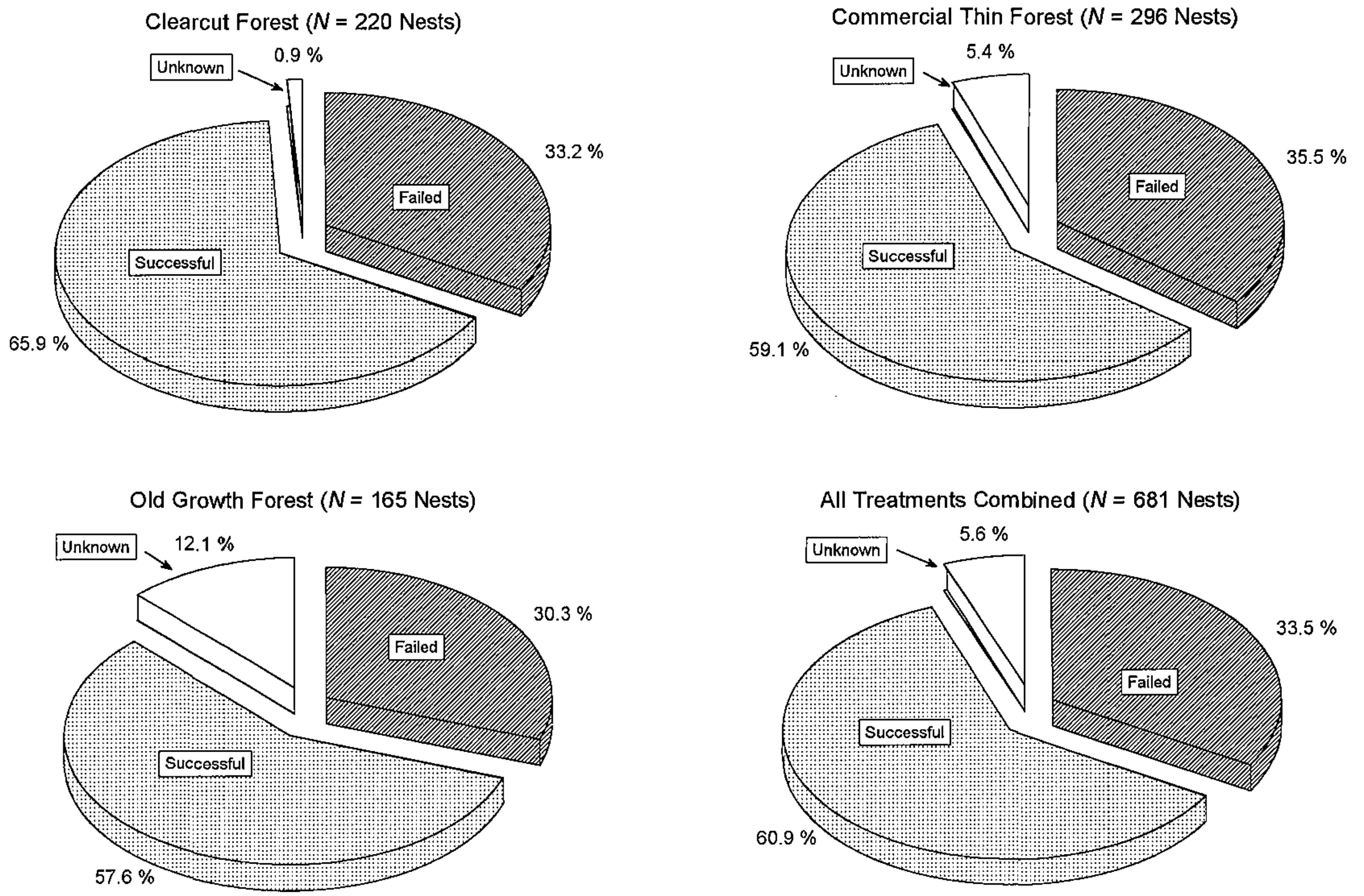
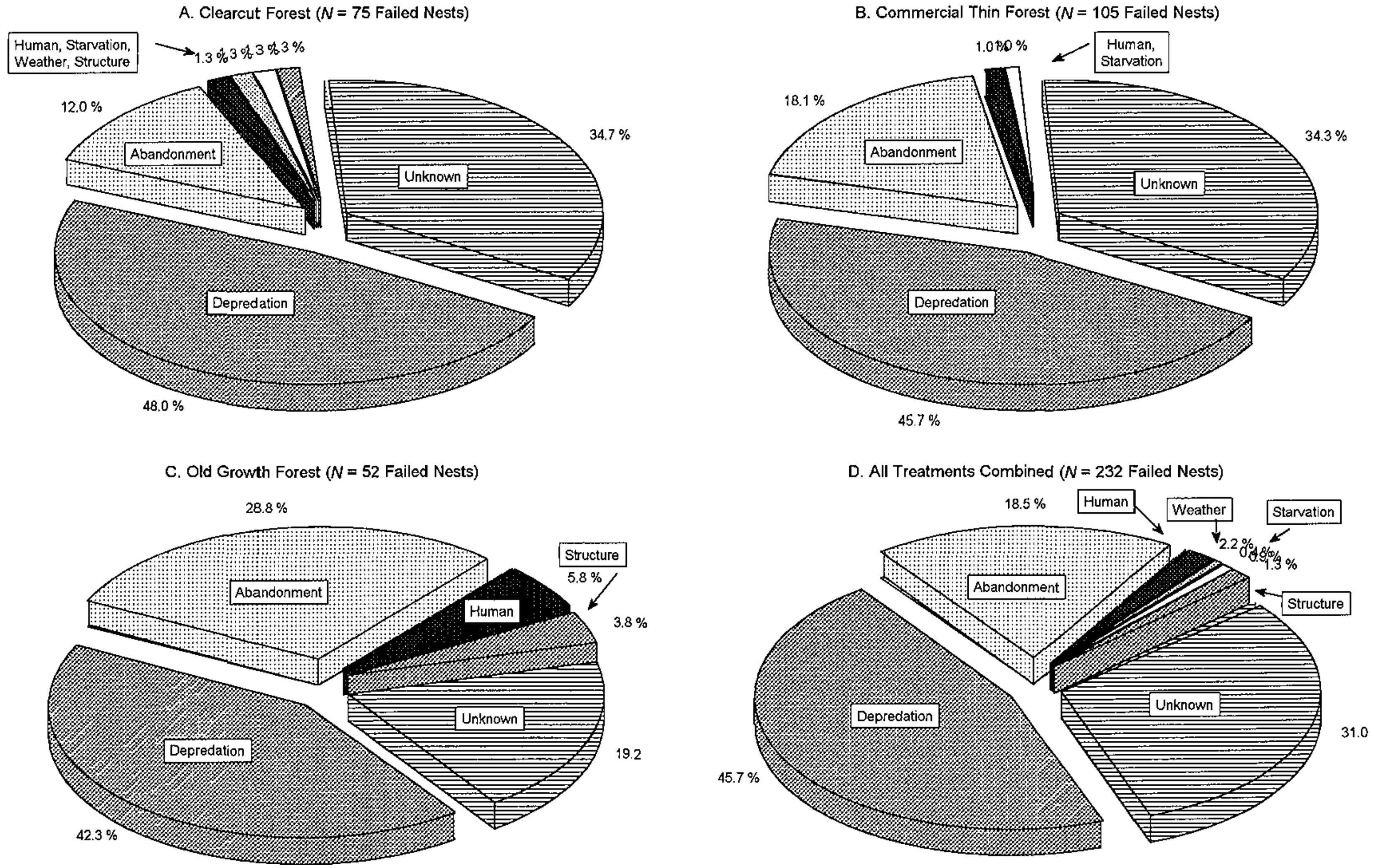


Figure 6. Summary of reasons for nest failure for 232 failed nests that were found and monitored in the southwestern Washington Cascades, 1998–1999.



Human = observer disturbance; Starvation = insufficient food; Weather = adverse weather; Structure = collapsed nest/supporting branches species for which we had sufficient data: (1) productivity per nest (number of young fledged per nest); (2) Mayfield nest success (Mayfield estimates of nest survivorship); and (3) productivity per unit area (number young fledged per 32 ha study plot). Per-capita reproduction refers to those measures of reproductive success that are calculated on a per nest or per bird-pair basis. That is, the individual nest (or bird-pair) is the unit of measure upon which mean values of success are calculated within each sample study plot. Both productivity per nest and Mayfield nest success are types of per-capita reproduction.

3.2.2. *Nest-level productivity* - For each species at each study plot, avian productivity on a per-nest basis was calculated as the mean number of young fledged per nest per two years by dividing the total number of young produced by the total number of nests monitored in 1998 and1999 combined. Nest-level productivity measures were computed as means per plot; that is study plots were the sample units, not individual nests within plots. Individual nests within a plot may not be independent of one another and using them as if they were may be a form of pseudoreplication.

3.2.3. *Mayfield nest success* - For each species at each study plot, we calculated nest success on a per-nest basis using the Mayfield (1975) estimate. Mayfield nest success is calculated as the probability that a nest will survive to fledge at least one host young. The Mayfield method corrects for biases in the probability of nest survivorship that might result when nests are not observed on a daily basis throughout the entire nesting cycle. We considered the first observation day as the first day of incubation (if the nest was found before incubation began) or the day the nest was located (if the nest was located after incubation had begun). For each species for which the fate of nests could reliably be determined (n = 18), we computed daily mortality across the nesting cycle as total number of failures divided by total number of observation days pooled across all nests within a study plot (as in Donovan et al. 1995, Burke and Nol 2000). Daily survival was calculated as (1 - daily mortality) for each species in each study plot. Overall nest success was based on the estimate of daily success raised to the exponent that reflects average length of the entire nesting cycle (Mayfield 1975). Values for average length of the nesting cycle for each species examined were obtained from the primary literature. Overall measures of nest success represent the probability that a nest will survive to successfully fledge one young.

3.2.4. *Area-level productivity* - Ideally, one would find all nests of a species within a study area and be able to compute avian productivity as the total number of young fledged. Such a parameter would presumably be one of the ultimate measures of habitat quality. Unfortunately, however, not all nests within a study area can be found. One way to obtain an "index" of area productivity would be to simply multiply the number of nests found for a species by nest-level productivity (defined above). To be an unbiased index, however, such an approach rests on the assumption that the probability of finding a nest does not vary from plot to plot. We have serious reservations about such an assumption, and indeed, analyses of our own data suggested that nests of some species (e.g., Winter Wren; *unpubl. data*) were more difficult to find in some treatments (e.g., old-growth forest) compared with others (e.g., commercial thins). Moreover, when questioned about this assumption directly, experienced nest searchers also raised doubts about its validity (J. M. Soules, *pers. comm.*). Therefore, we computed what we believe to be a relatively unbiased index of area productivity using spot-mapping data. We made the assumption that each territory mapped for a species contained a nest and calculated area-level productivity by multiplying territory numbers by nest-level productivity. This method yielded the number of young produced per spot-mapping grid (12 ha), which we then simply extrapolated to the study plot level (32 ha). As far as we are aware, ours is the first study to compute reproductive success in this way. We realize that not all territories may necessarily contain nests and that the proportion that do might vary from stand to stand. However, given the importance of generating an area-level measure of productivity to address the proposed objectives of this study, we consider our rationale and methods justified. Furthermore, we rarely found nests unassociated with territories, which suggests that we missed few territories during spot mapping.

3.3. Results and Discussion

We limit our analyses of relative avian abundance and bird density to point-count data collected within 100 m of observers and spot-mapping data, respectively; these data have been previously reported (see section 2, above). We chose to use count data collected over 100 m rather than the canonical 50 m in our analyses for two main reasons. Firstly, we wanted to remain consistent with our earlier analyses of correlations between abundance and density where we used bird detections made within 100 m of observers. Data collected within a 100 m radius also were used to estimate density using program DISTANCE. Our rationale for using 100 m data rather than 50 m data was that the greater distance effectively quadrupled the area sampled for birds within each forest stand (3.14 ha [100-m radius] vs. 0.80 ha [50-m radius]). Secondly, correlation analyses between measures of relative abundance calculated using 50- and 100-m radii data indicated the two variables to be highly correlated (R^2 = 0.96, $P < 0.0001$, $n = 37$ species; Fig. 7). Individual correlations for 37 species included in analyses are summarized (Table 10) and indicate that the abundance of birds at 50 and 100 m radii was not significantly correlated ($P > 0.10$) for only two of the 37 species (Northern Pygmy-Owl and Ruffed Grouse).

Figure 7. Correlation between relative avian abundance calculated using both 50- and 100-m radius point-count data for 37 bird species.

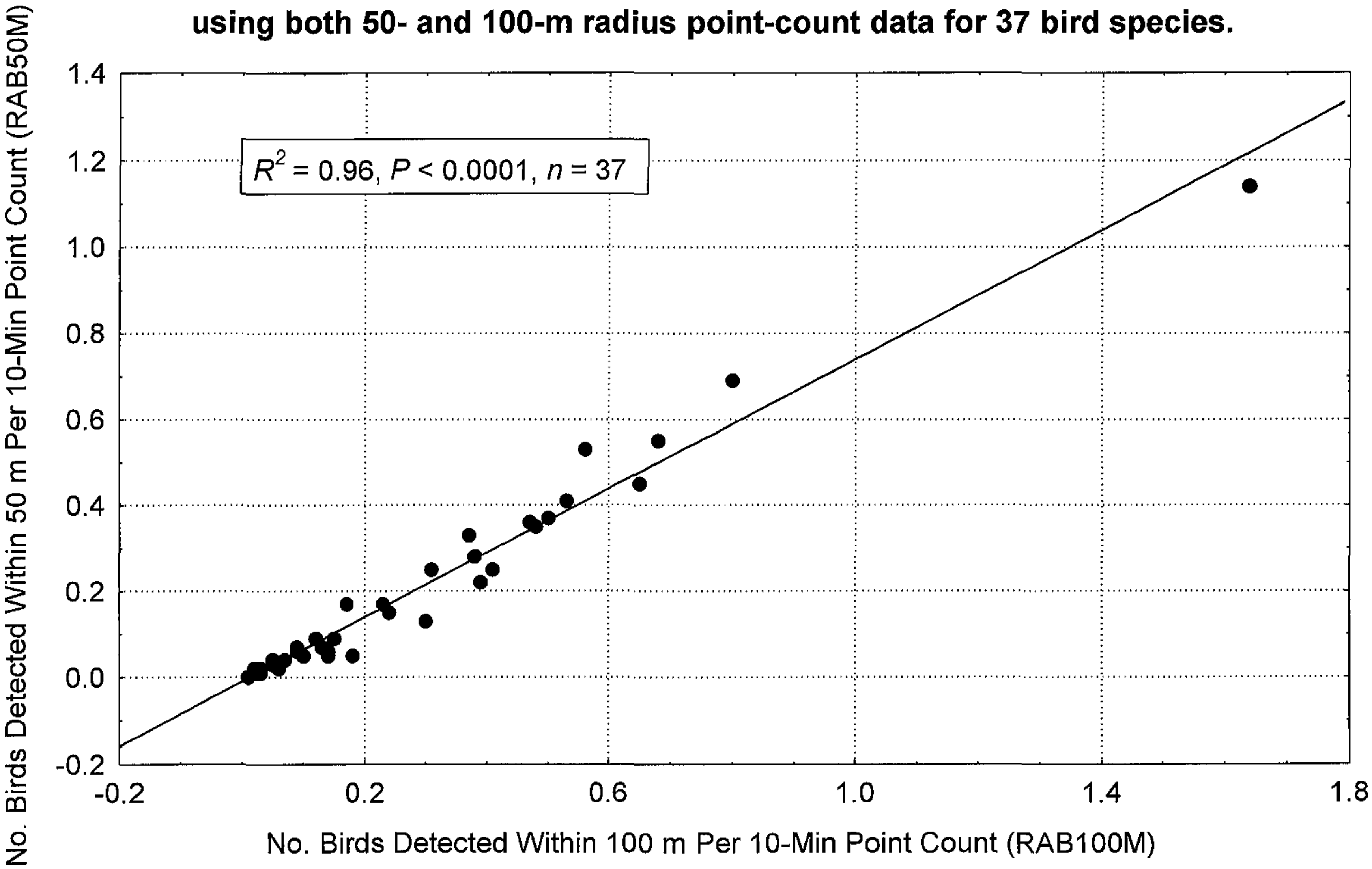


Table 10. Comparison of relative avian abundance estimates calculated using 50-m radius point-count data (RAB50M) and 100-m radius point-count data (RAB100M) for 37 bird species detected in forests of the southwest Cascade Mountains of Washington, 1998–1999.

	Mean ± SE No. Birds Detected Per 10-Min Point Count		Correlation Analyses		
Bird Species	Within 50 m (RAB50M)	Within 100 m (RAB100M)	*n*	*r*	*P*
American Goldfinch[a]	0.07 ± 0.07	0.09 ± 0.09	4	1.00	<0.0001
American Robin	0.22 ± 0.04	0.39 ± 0.06	12	0.95	<0.0001
Bewick's Wren	0.04 ± 0.02	0.07 ± 0.03	5	0.98	<0.01
Black-headed Grosbeak[a]	0.06 ± 0.03	0.09 ± 0.04	9	0.76	<0.05
Blue Grouse[a]	0.03 ± 0.02	0.05 ± 0.03	7	0.99	<0.0001
Brown Creeper	0.25 ± 0.06	0.31 ± 0.07	10	0.99	<0.0001
Chestnut-backed Chickadee	0.53 ± 0.08	0.56 ± 0.09	11	0.99	<0.0001
Cedar Waxwing[a]	0.02 ± 0.01	0.03 ± 0.02	6	0.82	<0.05
Common Raven[a]	0.00 ± 0.00	0.01 ± 0.01	12	0.71	<0.01
Common Yellowthroat	0.69 ± 0.44	0.80 ± 0.50	3	1.00	<0.01
Dark-eyed Junco[a]	0.36 ± 0.10	0.47 ± 0.12	12	0.98	<0.0001
Evening Grosbeak[a]	0.04 ± 0.02	0.05 ± 0.03	12	0.98	<0.0001
Golden-crowned Kinglet	0.33 ± 0.08	0.37 ± 0.09	11	1.00	<0.0001
Gray Jay[a]	0.09 ± 0.03	0.15 ± 0.04	10	0.81	<0.01
Hairy Woodpecker	0.09 ± 0.02	0.12 ± 0.02	12	0.98	<0.0001
Hermit/Townsend's Warbler	0.25 ± 0.07	0.41 ± 0.11	10	0.99	<0.0001
MacGillivray's Warbler	0.35 ± 0.13	0.48 ± 0.16	7	0.96	<0.0001
Northern Flicker	0.02 ± 0.01	0.06 ± 0.01	12	0.90	<0.0001
Northern Pygmy-Owl[a]	0.01 ± 0.01	0.03 ± 0.01	6	0.72	0.11
Orange-crowned Warbler	0.37 ± 0.13	0.50 ± 0.19	7	0.99	<0.0001
Pileated Woodpecker	0.01 ± 0.01	0.02 ± 0.01	6	0.86	<0.05
Pacific-slope Flycatcher	0.45 ± 0.11	0.65 ± 0.14	11	0.98	<0.0001

Red-breasted Nuthatch[a]	0.06 ± 0.03	0.14 ± 0.05	10	0.94	<0.0001
Red-breasted Sapsucker	0.02 ± 0.01	0.02 ± 0.01	4	0.99	<0.05
Ruffed Grouse	0.02 ± 0.01	0.03 ± 0.01	3	0.76	0.45
Rufous Hummingbird[a]	0.17 ± 0.07	0.17 ± 0.07	10	1.00	<0.0001
Song Sparrow[a]	0.41 ± 0.21	0.53 ± 0.26	10	0.86	<0.001
Spotted Towhee	0.28 ± 0.18	0.38 ± 0.15	9	1.00	<0.0001
Steller's Jay[a]	0.05 ± 0.03	0.14 ± 0.05	12	0.56	0.06
Swainson's Thrush	0.15 ± 0.04	0.24 ± 0.06	12	0.97	<0.0001
Varied Thrush	0.13 ± 0.03	0.30 ± 0.07	12	0.96	<0.0001
Warbling Vireo[a]	0.05 ± 0.03	0.10 ± 0.04	6	0.81	0.05
White-crowned Sparrow	0.05 ± 0.02	0.18 ± 0.05	8	0.89	<0.01
Western Tanager[a]	0.07 ± 0.03	0.13 ± 0.06	10	0.98	<0.0001
Willow Flycatcher	0.55 ± 0.22	0.68 ± 0.26	7	0.99	<0.0001
Wilson's Warbler	0.17 ± 0.03	0.23 ± 0.05	12	0.96	<0.0001
Winter Wren	1.14 ± 0.22	1.64 ± 0.27	11	0.98	<0.0001

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[a] Indicates correlation analyses performed using non-parametric Spearman rank correlation analysis due to nonnormal data. Otherwise, values of *r* are parametric Pearson product-moment correlation coefficients. Tests for normality were conducted using Shapiro-Wilks' W Test.

The three measures of reproductive success are summarized by forest treatment for 18 species and 10 species' groups (Table 11). Correlation analyses among the five population parameters (abundance [RAB100M], density [DENSPOT], nest-level productivity [NESTPROD], nest success [NESTSURV], and area productivity [AREAPROD]) were conducted for the 11 species for which we had sufficient data (i.e., measures of each of these five variables in at least three study plots). Seven species included in Table 11 (Common Yellowthroat, Hermit/Townsend's Warbler, MacGillivray's Warbler, Red-breasted Nuthatch, Swainson's Thrush, White-crowned Sparrow, Wilson's Warbler) could not be included in analyses, primarily because we lacked density estimates derived from spot mapping for these species. We decided to include DENSPOT but not density derived from DISTANCE (DENDIST) in these correlation analyses for several reasons: (1) DENDIST and DENSPOT had been previously shown to be highly correlated with one another (see section 2.4.2., above); (2) we believed DENSPOT to be a more accurate measure of bird density compared with DENDIST; (3) more researchers have used spot mapping to estimate density than have used DISTANCE software; and (4) although AREAPROD is a function of DENSPOT (see section 3.2.4., above), DENDIST suffers from the same potential problems of autocorrelation because DENDIST is a function of RAB100M (i.e., relative abundance data were used to calculate density using program DISTANCE). Note also that AREAPROD is a function of two variables (DENSPOT and NESTPROD), therefore rendering any simple linear correlations between AREAPROD and DENSPOT unlikely.

3.3.1. ***Correlations among abundance, density, and per-capita reproduction*** - Of the 11 species for which we compared abundance (RAB100M), density (DENSPOT), and nest-level reproductive success (NESTPROD and NESTSURV), the majority (American Robin, Brown Creeper, Dark-eyed Junco, Orange-crowned Warbler, Song Sparrow, Spotted Towhee) exhibited no significant correlations (Fig. 8). In other words, our measures of reproductive success on a per-capita (nest-level) basis appeared to be density independent: regardless of changes in abundance or density, the number of young fledged per nest, or the probability of nest survivorship, remained constant. This pattern is perhaps illustrated best by data for the Song Sparrow (Fig. 8g), where scatter diagrams for RAB100M vs. NESTPROD, RAB100M vs. NESTSURV, DENSPOT vs. NESTPROD, and DENSPOT vs. NESTSURV show "flat-line relationships."

Two species exhibited one significant positive correlation among these variables: (1) RAB100M vs. NESTSURV for the Willow Flycatcher (Fig. 8j); and (2) DENSPOT vs. NESTPROD for the Winter Wren (Fig. 8k). These results suggest that for these two species, per-capita reproductive success was inversely density-dependent: the more birds there were per unit area, the greater the probability of nest success (for the Willow Flycatcher) or the more young produced per nest (for the Winter Wren). For such species with inversely density dependent per-capita

Table 11. Mean (±SE) values and associated sample sizes of the three variables calculated to measure reproductive success for all species and species' groups, summarized by forest treatment.

	Forest	No. Young Fledged / Nest[a]		Mayfield Nest Success[b]		No. Young Fledged / Plot[c]	
Species or Species' Group	Treatment	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*
American Robin	Clearcut	1.06 ± 0.63	4	0.35 ± 0.21	4	8.79 ± 4.76	3
	Commercial Thin	1.86 ± 0.43	4	0.45 ± 0.20	4	12.77 ± 2.66	4
	Old Growth	2.00 ± 2.00	2	1.00 ± 0.00	1	0.00 ± 0.00	1
Brown Creeper	Clearcut	--[d]	0	--	0	--	0
	Commercial Thin	3.53 ± 0.86	4	0.53 ± 0.27	4	32.49 ± 12.69	3
	Old Growth	4.85 ± 0.54	4	0.97 ± 0.03	4	52.83 ± 11.94	4
Chestnut-backed Chickadee	Clearcut	0.00 ± 0.00	1	--	0	--	0
	Commercial Thin	3.08 ± 0.58	3	1.00 ± 0.00	3	74.76 ± 0.00	1
	Old Growth	5.92 ± 0.58	3	0.92 ± 0.08	3	55.40 ± 20.69	2
Common Yellowthroat	Clearcut	2.34 ± 0.03	2	0.51 ± 0.05	2	71.55 ± 30.33	2
	Commercial Thin	--	0	--	0	--	0
	Old Growth	--	0	--	0	--	0
Dark-eyed Junco	Clearcut	2.53 ± 0.35	3	0.81 ± 0.09	3	66.01 ± 12.00	3
	Commercial Thin	2.03 ± 0.38	4	0.46 ± 0.19	4	41.43 ± 15.23	4
	Old Growth	2.25 ± 1.25	2	1.00 ± 0.00	2	28.04 ± 0.00	1
Hermit/Townsend's Warbler	Clearcut	--	0	--	0	--	0
	Commercial Thin	4.50 ± 0.00	1	1.00 ± 0.00	1	90.11 ± 0.00	1
	Old Growth	--	0	--	0	--	0
MacGillivray's Warbler	Clearcut	2.67 ± 0.00	1	0.09 ± 0.00	1	85.44 ± 0.00	1
	Commercial Thin	1.50 ± 0.00	1	0.36 ± 0.00	1	4.01 ± 0.00	1
	Old Growth	--	0	--	0	--	0

Species or Species' Group	Forest Treatment	No. Young Fledged / Nest[a]		Mayfield Nest Success[b]		No. Young Fledged / Plot[c]	
		Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*
Orange-crowned Warbler	Clearcut	1.75 ± 1.75	2	0.51 ± 0.49	2	37.38 ± 37.38	2
	Commercial Thin	1.50 ± 0.00	1	0.42 ± 0.00	1	6.01 ± 0.00	1
	Old Growth	--	0	--	0	--	0
Pacific-slope Flycatcher	Clearcut	0.00 ± 0.00	1	--	0	--	0
	Commercial Thin	1.93 ± 0.36	4	0.63 ± 0.13	4	30.82 ± 3.93	4
	Old Growth	2.27 ± 0.93	4	0.58 ± 0.24	4	36.38 ± 14.00	4
Red-breasted Nuthatch	Clearcut	--	0	--	0	--	0
	Commercial Thin	5.67 ± 0.17	3	1.00 ± 0.00	3	--	0
	Old Growth	4.63 ± 1.38	2	1.00 ± 0.00	2	48.06 ± 0.00	1
Song Sparrow	Clearcut	2.64 ± 0.21	4	0.75 ± 0.15	4	68.37 ± 23.21	4
	Commercial Thin	1.00 ± 0.00	1	0.18 ± 0.00	1	4.01 ± 0.00	1
	Old Growth	--	0	--	0	--	0
Spotted Towhee	Clearcut	1.00 ± 0.58	4	0.26 ± 0.15	4	16.02 ± 9.31	4
	Commercial Thin	0.00 ± 0.00	1	0.32 ± 0.00	1	0.00 ± 0.00	1
	Old Growth	--	0	--	0	--	0
Swainson's Thrush	Clearcut	2.50 ± 0.50	2	1.00 ± 0.00	2	10.68 ± 0.00	1
	Commercial Thin	3.00 ± 2.00	2	0.83 ± 0.17	2	5.34 ± 0.00	1
	Old Growth	3.00 ± 0.00	1	1.00 ± 0.00	1	--	0
Varied Thrush	Clearcut	3.00 ± 0.00	1	1.00 ± 0.00	1	16.02 ± 0.00	1
	Commercial Thin	1.00 ± 1.00	2	0.50 ± 0.50	2	16.02 ± 0.00	1
	Old Growth	1.54 ± 0.40	3	0.55 ± 0.26	3	12.07 ± 2.26	3
White-crowned Sparrow	Clearcut	2.50 ± 0.50	2	1.00 ± 0.00	2	16.02 ± 0.00	1
	Commercial Thin	--	0	--	0	--	0
	Old Growth	--	0	--	0	--	0

Species or Species' Group	Forest Treatment	No. Young Fledged / Nest[a]		Mayfield Nest Success[b]		No. Young Fledged / Plot[c]	
		Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*
Willow Flycatcher	Clearcut	2.14 ± 0.16	3	0.67 ± 0.06	3	55.46 ± 11.65	3
	Commercial Thin	--	0	--	0	--	0
	Old Growth	--	0	--	0	--	0
Wilson's Warbler	Clearcut	3.00 ± 0.00	1	1.00 ± 0.00	1	--	0
	Commercial Thin	3.00 ± 1.53	3	0.78 ± 0.22	3	16.69 ± 16.69	2
	Old Growth	0.00 ± 0.00	1	0.14 ± 0.00	1	--	0
Winter Wren	Clearcut	2.33 ± 0.00	1	0.57 ± 0.00	1	93.45 ± 0.00	1
	Commercial Thin	2.24 ± 0.14	4	0.37 ± 0.05	4	126.60 ± 38.49	4
	Old Growth	1.74 ± 0.59	4	0.26 ± 0.14	4	97.08 ± 47.40	4
Resident Birds	Clearcut	1.82 ± 0.36	4	0.62 ± 0.08	4	32.07 ± 5.37	4
	Commercial Thin	2.88 ± 0.27	4	0.68 ± 0.04	4	51.64 ± 8.69	4
	Old Growth	3.35 ± 0.19	4	0.82 ± 0.03	4	54.36 ± 14.82	4
Migrant Birds	Clearcut	1.88 ± 0.16	4	0.68 ± 0.12	4	55.11 ± 15.14	4
	Commercial Thin	2.62 ± 0.52	4	0.70 ± 0.08	4	34.10 ± 10.68	4
	Old Growth	2.31 ± 0.73	4	0.71 ± 0.18	4	36.39 ± 14.00	4
Open-cup-Nesting Birds	Clearcut	1.75 ± 0.12	4	0.61 ± 0.05	4	37.27 ± 11.68	4
	Commercial Thin	2.33 ± 0.15	4	0.65 ± 0.06	4	24.72 ± 7.18	4
	Old Growth	1.88 ± 0.50	4	0.66 ± 0.15	4	22.72 ± 7.28	4
Ground-Nesting Birds	Clearcut	2.49 ± 0.84	3	0.76 ± 0.19	3	59.01 ± 15.53	3
	Commercial Thin	3.00 ± 0.78	4	0.60 ± 0.11	4	38.90 ± 16.25	4
	Old Growth	2.25 ± 1.25	2	1.00 ± 0.00	2	28.04 ± 0.00	1

	Forest	No. Young Fledged / Nest[a]		Mayfield Nest Success[b]		No. Young Fledged / Plot[c]	
Species or Species' Group	Treatment	Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*
Cavity-Nesting Birds	Clearcut	1.29 ± 0.65	3	0.60 ± 0.30	3	93.45 ± 0.00	1
	Commercial Thin	3.14 ± 0.42	4	0.73 ± 0.06	4	89.26 ± 22.01	4
	Old Growth	3.91 ± 0.23	4	0.84 ± 0.03	4	76.28 ± 22.24	4
Foliage-Gleaning Birds	Clearcut	1.77 ± 0.08	4	0.60 ± 0.06	4	47.10 ± 14.74	4
	Commercial Thin	2.74 ± 0.20	4	0.72 ± 0.08	4	63.46 ± 21.83	4
	Old Growth	2.69 ± 0.17	4	0.55 ± 0.08	4	62.18 ± 20.13	4
Ground-Feeding Birds	Clearcut	2.05 ± 0.59	4	0.61 ± 0.10	4	40.93 ± 15.63	4
	Commercial Thin	2.66 ± 0.61	4	0.56 ± 0.07	4	27.10 ± 6.97	4
	Old Growth	2.08 ± 0.94	3	1.00 ± 0.00	3	14.08 ± 14.01	2
Bark-Gleaning Birds	Clearcut	3.00 ± 1.00	2	1.00 ± 0.00	2	--	0
	Commercial Thin	3.35 ± 0.66	4	0.75 ± 0.10	4	32.49 ± 12.69	3
	Old Growth	4.16 ± 0.38	4	0.99 ± 0.01	4	48.54 ± 8.72	4
Aerial-Feeding Birds	Clearcut	1.84 ± 0.30	4	0.79 ± 0.08	4	55.46 ± 11.65	3
	Commercial Thin	1.43 ± 0.21	4	0.51 ± 0.07	4	30.81 ± 3.94	4
	Old Growth	2.08 ± 0.82	4	0.62 ± 0.23	4	36.39 ± 14.00	4
All Species Combined	Clearcut	1.84 ± 0.14	4	0.64 ± 0.06	4	45.68 ± 7.45	4
	Commercial Thin	2.79 ± 0.28	4	0.68 ± 0.05	4	44.40 ± 9.99	4
	Old Growth	3.06 ± 0.31	4	0.78 ± 0.03	4	49.80 ± 10.21	4

---

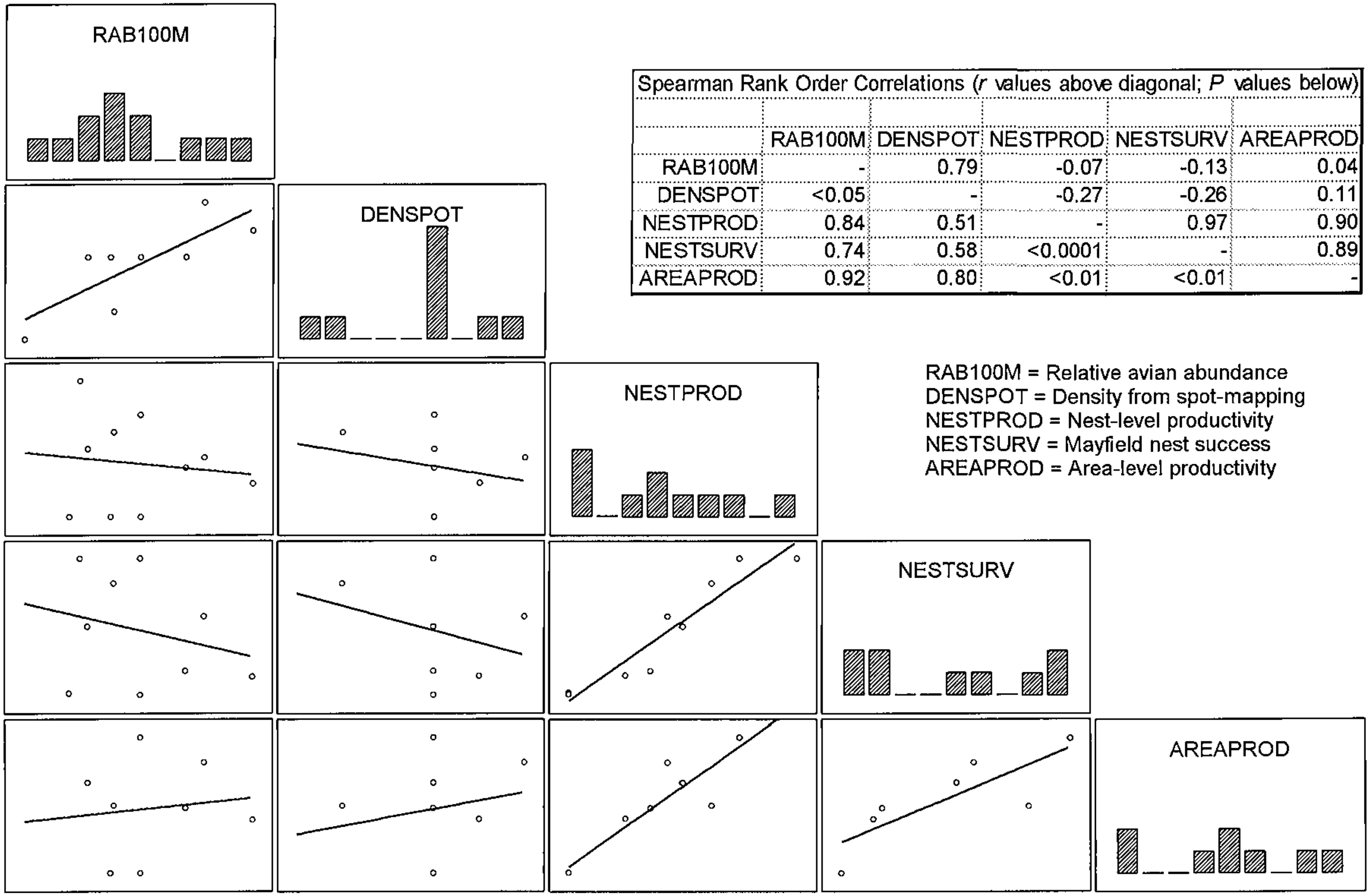
[a] No. young fledged / nest (NESTPROD) = Productivity per nest.

[b] Mayfield nest success (NESTSURV) = Nest survivorship (probability that a nest will “survive” to fledge at least one young).

[c] No. young fledged / unit area (AREAPROD) = Productivity per study plot (32 ha); calculated by multiplying extrapolated territory numbers by the mean number of young fledged per nest (see text for more details).

[d] Indicates insufficient data to compute variables.

Figure 8a. Correlation among relative abundance, density, and reproductive success for the American Robin.

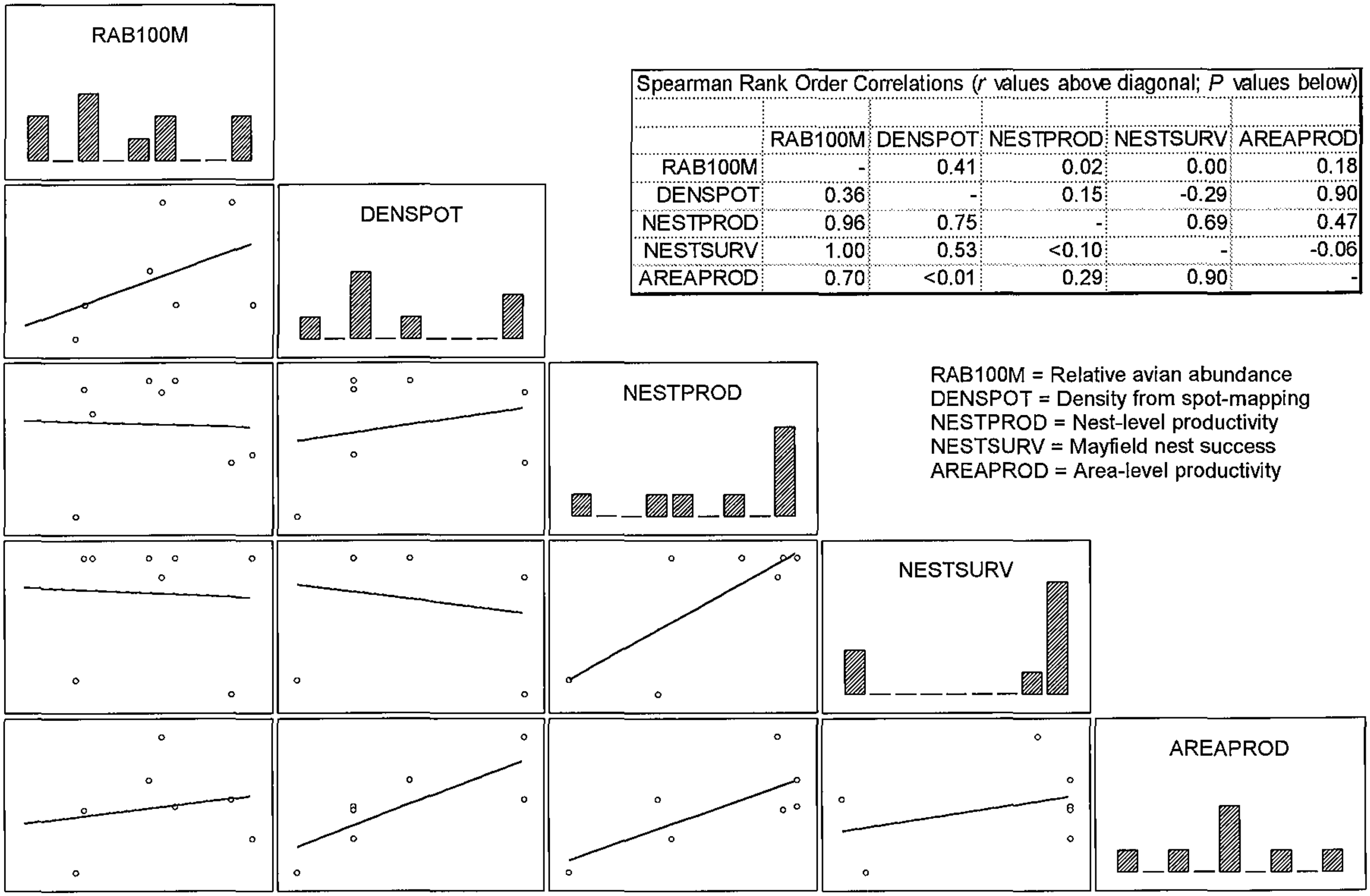


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.79	-0.07	-0.13	0.04
DENSPOT	<0.05	-	-0.27	-0.26	0.11
NESTPROD	0.84	0.51	-	0.97	0.90
NESTSURV	0.74	0.58	<0.0001	-	0.89
AREAPROD	0.92	0.80	<0.01	<0.01	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8b. Correlation among relative abundance, density, and reproductive success for the Brown Creeper.

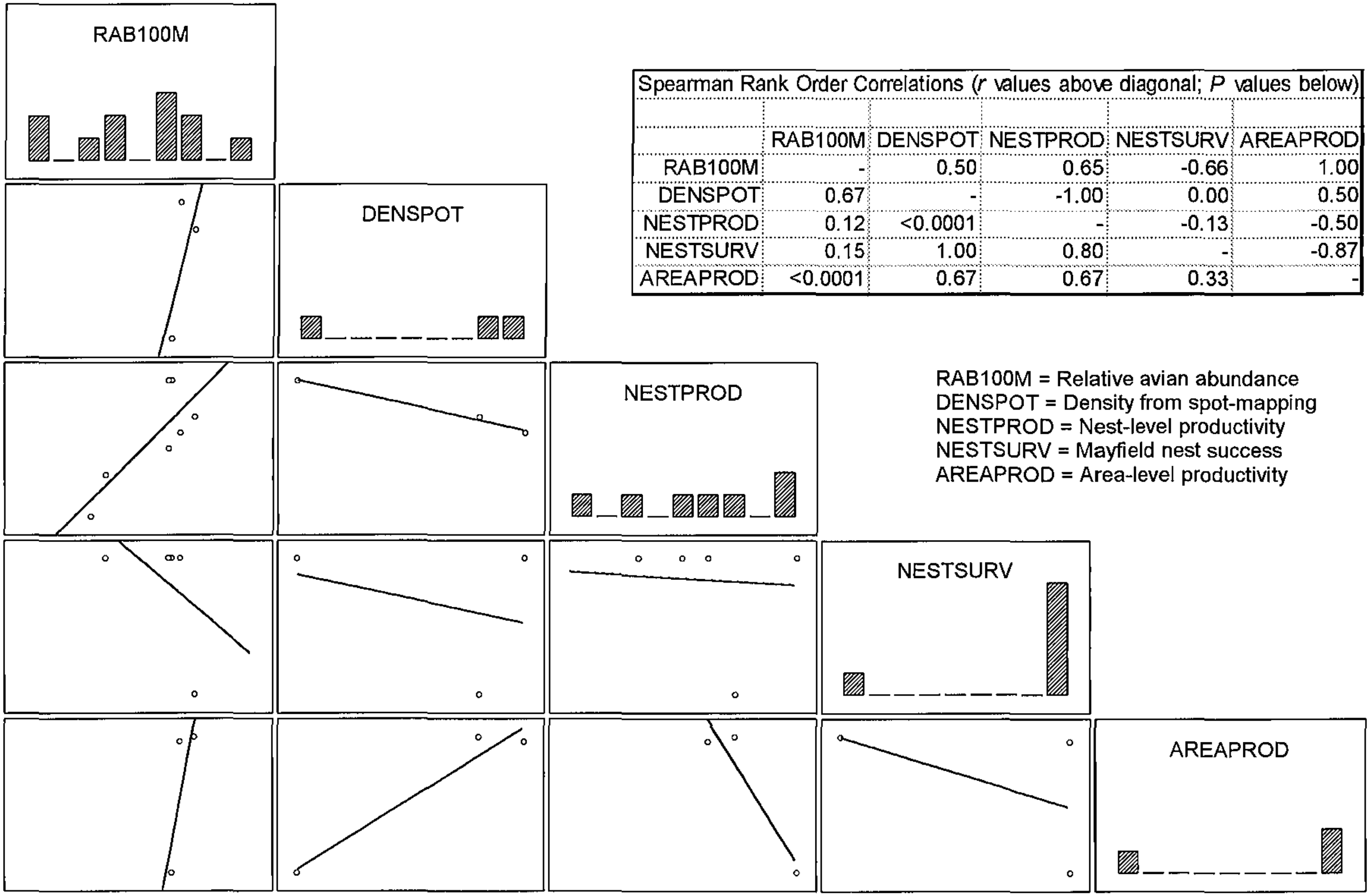


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.41	0.02	0.00	0.18
DENSPOT	0.36	-	0.15	-0.29	0.90
NESTPROD	0.96	0.75	-	0.69	0.47
NESTSURV	1.00	0.53	<0.10	-	-0.06
AREAPROD	0.70	<0.01	0.29	0.90	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8c. Correlation among relative abundance, density, and reproductive success for the Chestnut-backed Chickadee.

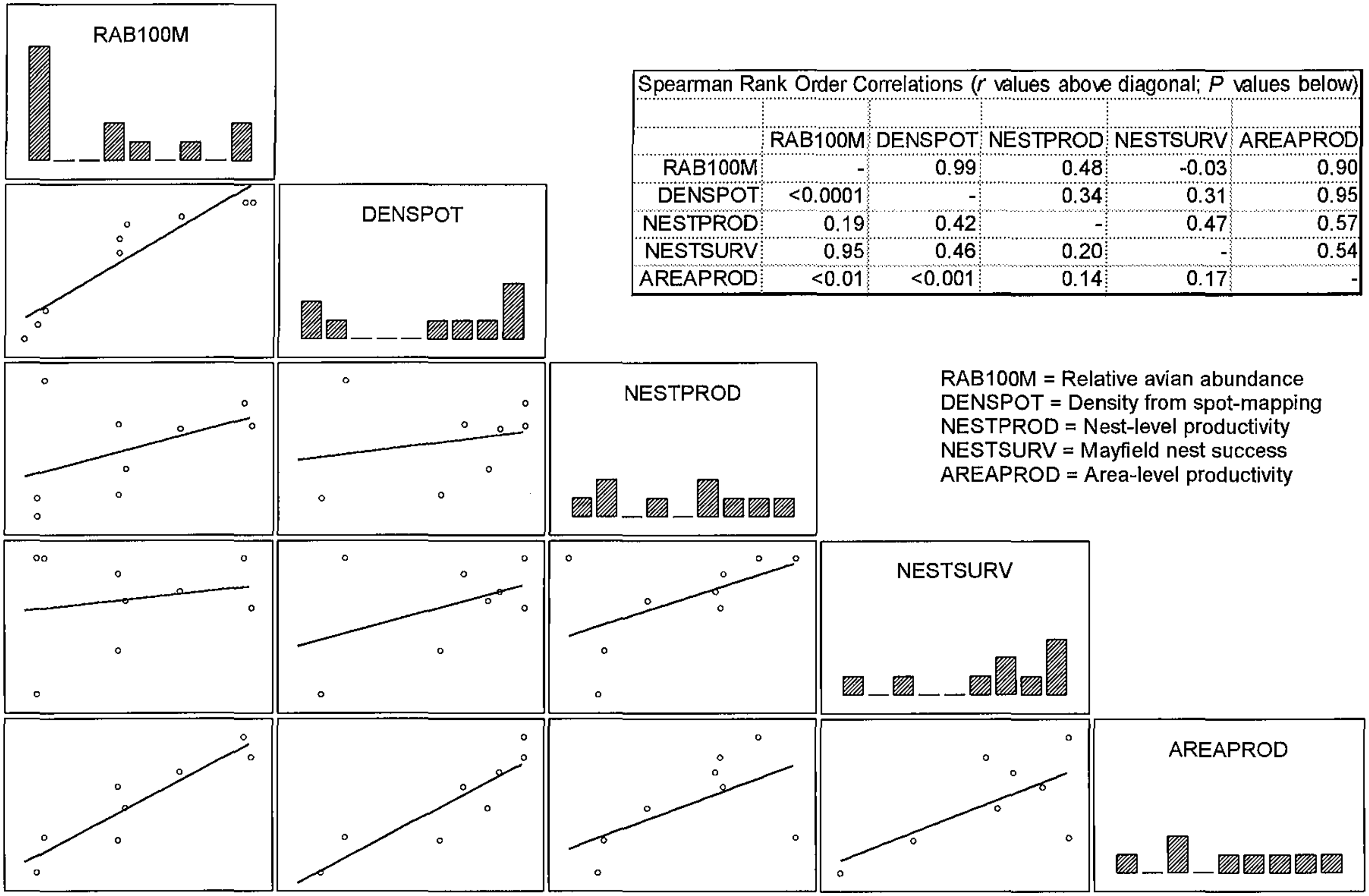


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.50	0.65	-0.66	1.00
DENSPOT	0.67	-	-1.00	0.00	0.50
NESTPROD	0.12	<0.0001	-	-0.13	-0.50
NESTSURV	0.15	1.00	0.80	-	-0.87
AREAPROD	<0.0001	0.67	0.67	0.33	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8d. Correlation among relative abundance, density, and reproductive success for the Dark-eyed Junco.

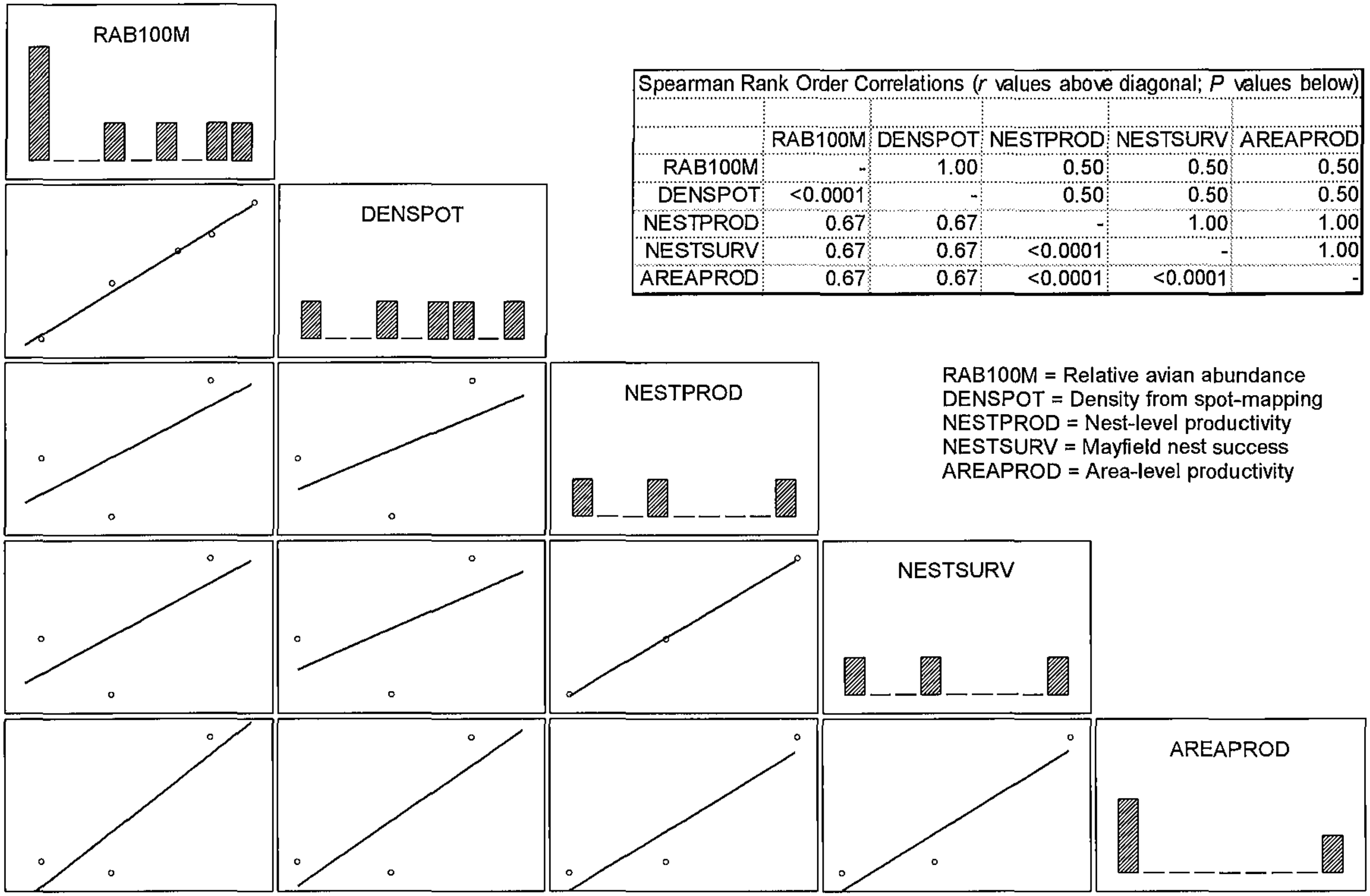


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.99	0.48	-0.03	0.90
DENSPOT	<0.0001	-	0.34	0.31	0.95
NESTPROD	0.19	0.42	-	0.47	0.57
NESTSURV	0.95	0.46	0.20	-	0.54
AREAPROD	<0.01	<0.001	0.14	0.17	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8e. Correlation among relative abundance, density, and reproductive success for the Orange-crowned Warbler.

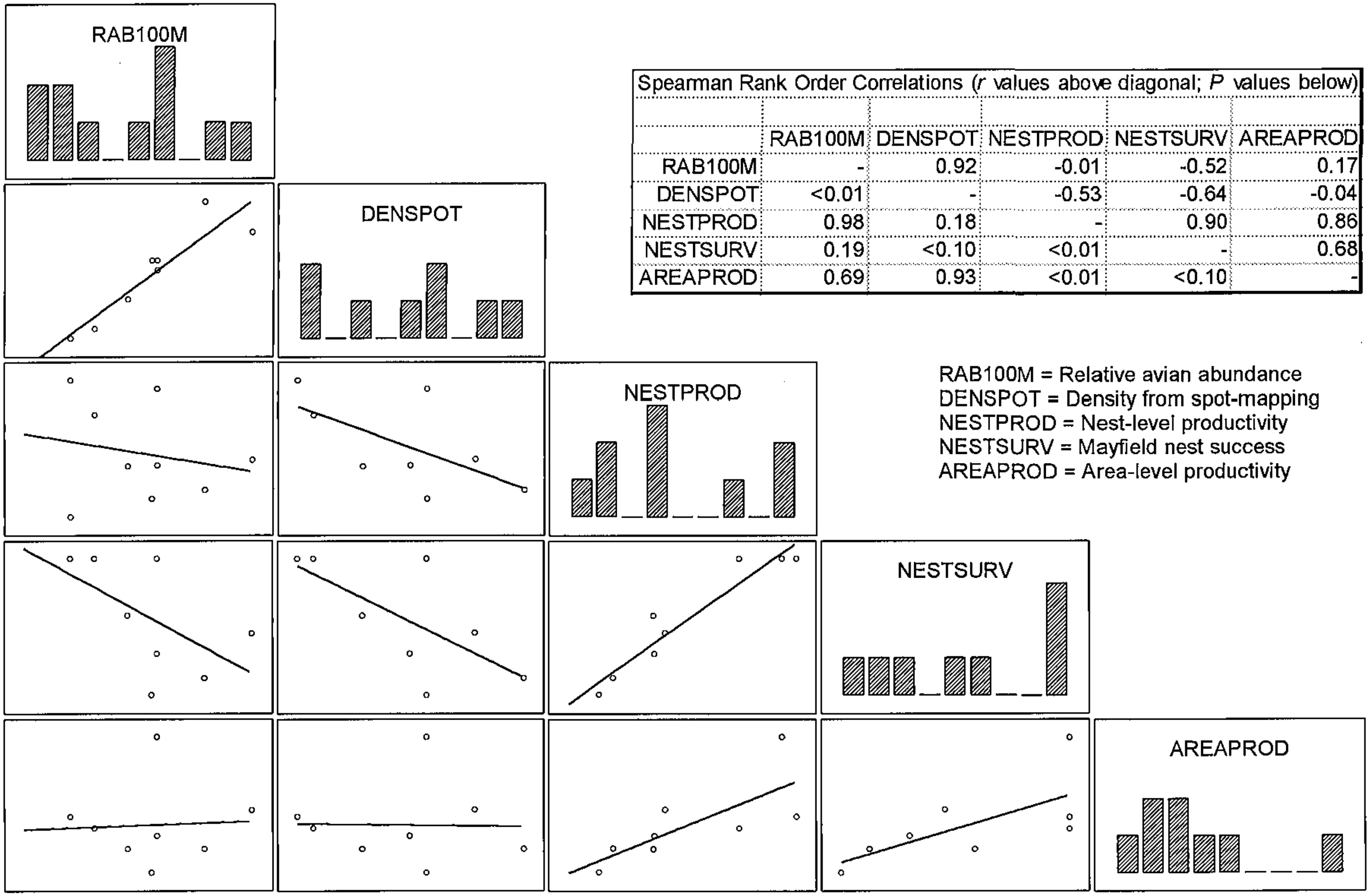


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	1.00	0.50	0.50	0.50
DENSPOT	<0.0001	-	0.50	0.50	0.50
NESTPROD	0.67	0.67	-	1.00	1.00
NESTSURV	0.67	0.67	<0.0001	-	1.00
AREAPROD	0.67	0.67	<0.0001	<0.0001	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8f. Correlation among relative abundance, density, and reproductive success for the Pacific-slope Flycatcher.

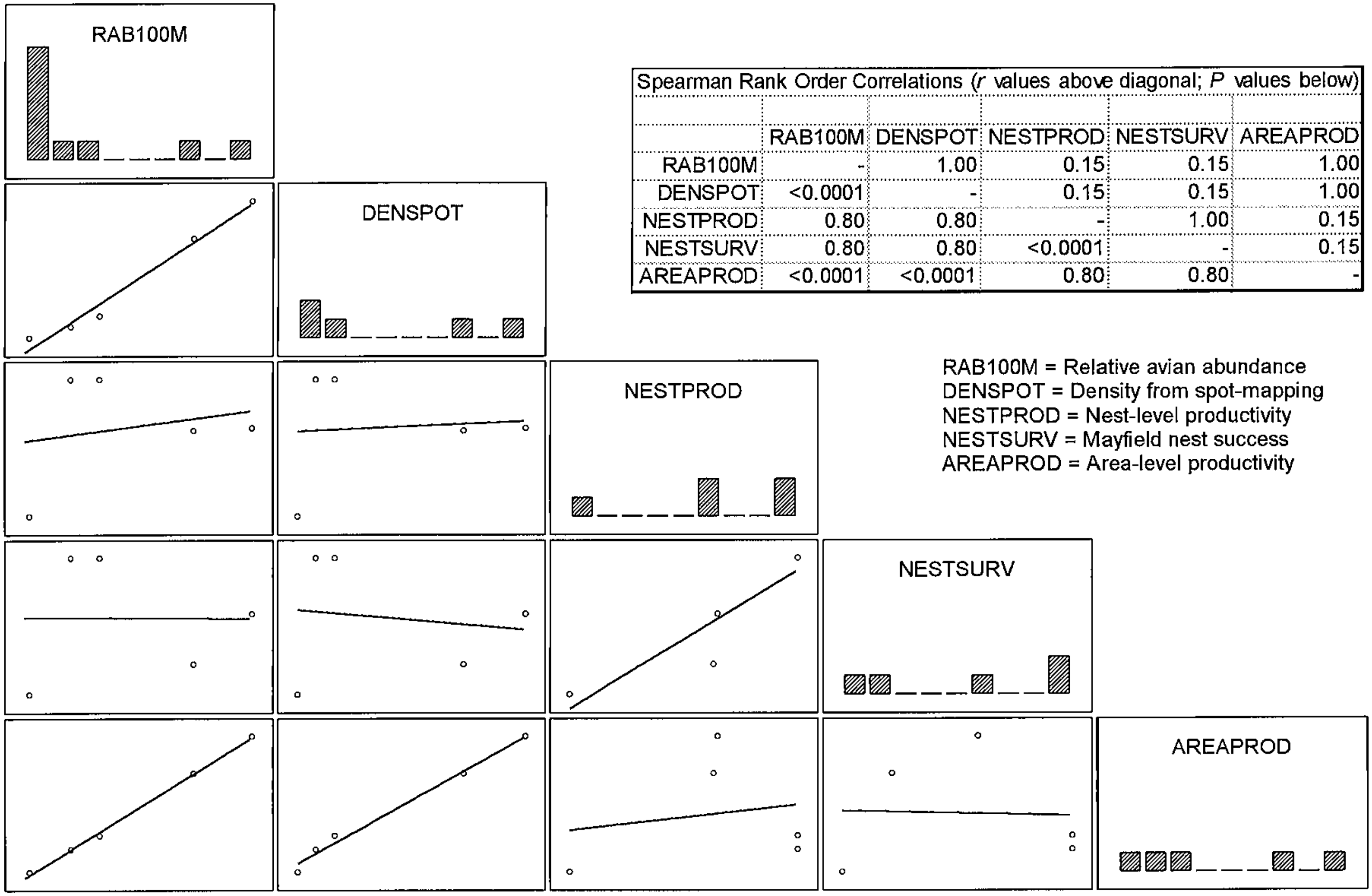


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.92	-0.01	-0.52	0.17
DENSPOT	<0.01	-	-0.53	-0.64	-0.04
NESTPROD	0.98	0.18	-	0.90	0.86
NESTSURV	0.19	<0.10	<0.01	-	0.68
AREAPROD	0.69	0.93	<0.01	<0.10	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8g. Correlation among relative abundance, density, and reproductive success for the Song Sparrow.

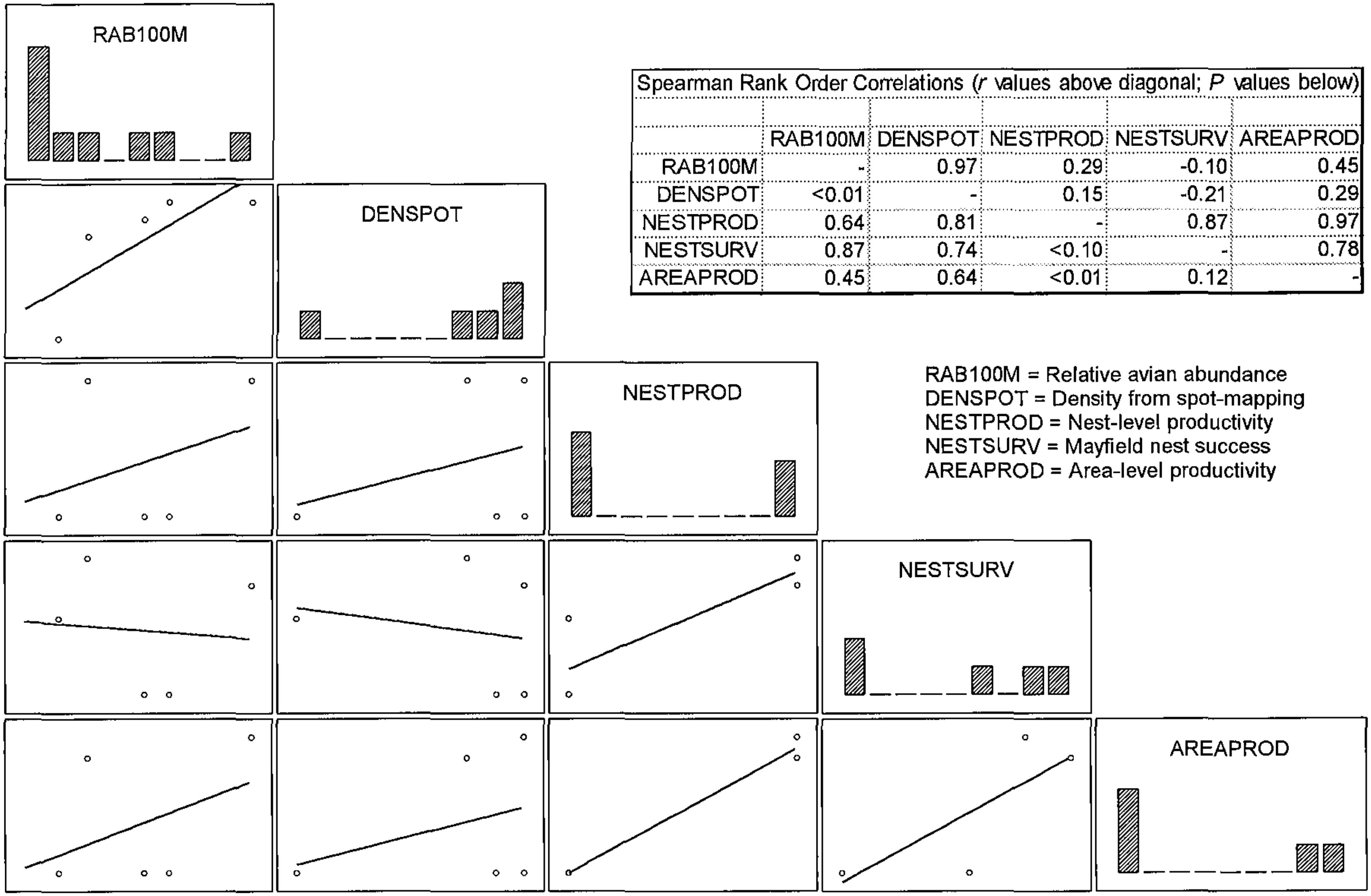


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	1.00	0.15	0.15	1.00
DENSPOT	<0.0001	-	0.15	0.15	1.00
NESTPROD	0.80	0.80	-	1.00	0.15
NESTSURV	0.80	0.80	<0.0001	-	0.15
AREAPROD	<0.0001	<0.0001	0.80	0.80	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8h. Correlation among relative abundance, density, and reproductive success for the Spotted Towhee.

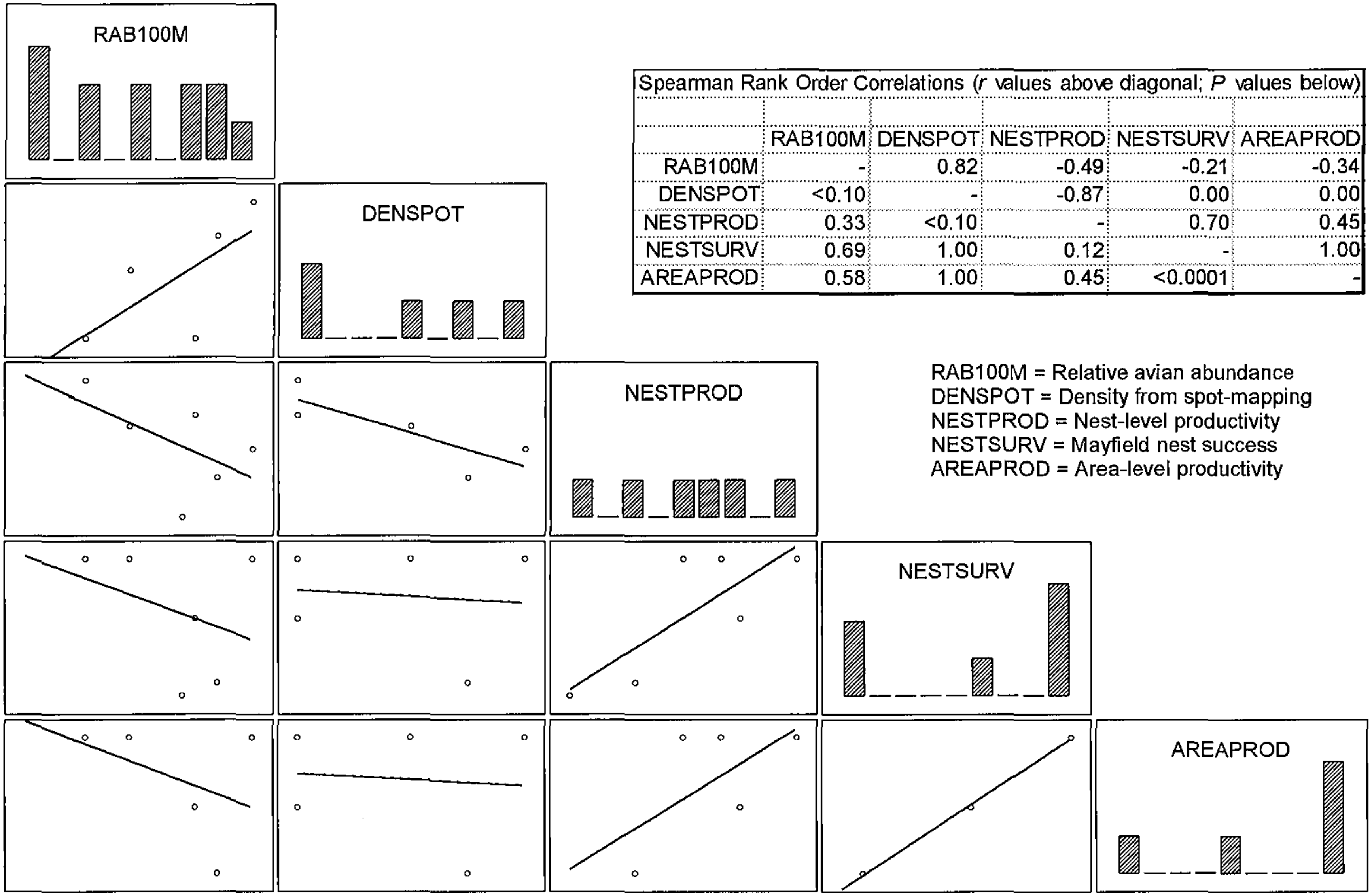


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.97	0.29	-0.10	0.45
DENSPOT	<0.01	-	0.15	-0.21	0.29
NESTPROD	0.64	0.81	-	0.87	0.97
NESTSURV	0.87	0.74	<0.10	-	0.78
AREAPROD	0.45	0.64	<0.01	0.12	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

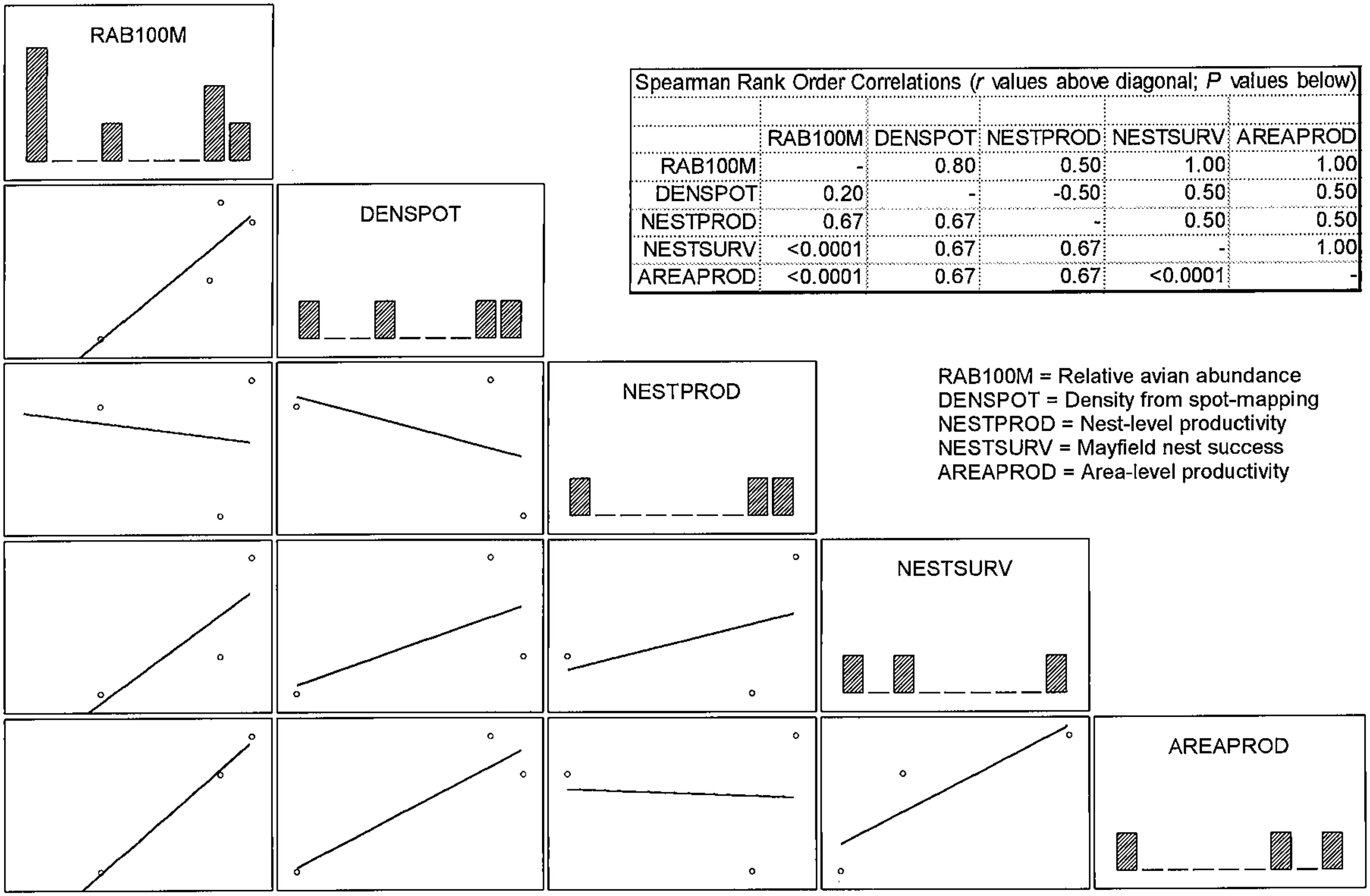
Figure 8i. Correlation among relative abundance, density, and reproductive success for the Varied Thrush.



Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.82	-0.49	-0.21	-0.34
DENSPOT	<0.10	-	-0.87	0.00	0.00
NESTPROD	0.33	<0.10	-	0.70	0.45
NESTSURV	0.69	1.00	0.12	-	1.00
AREAPROD	0.58	1.00	0.45	<0.0001	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8j. Correlation among relative abundance, density, and reproductive success for the Willow Flycatcher.

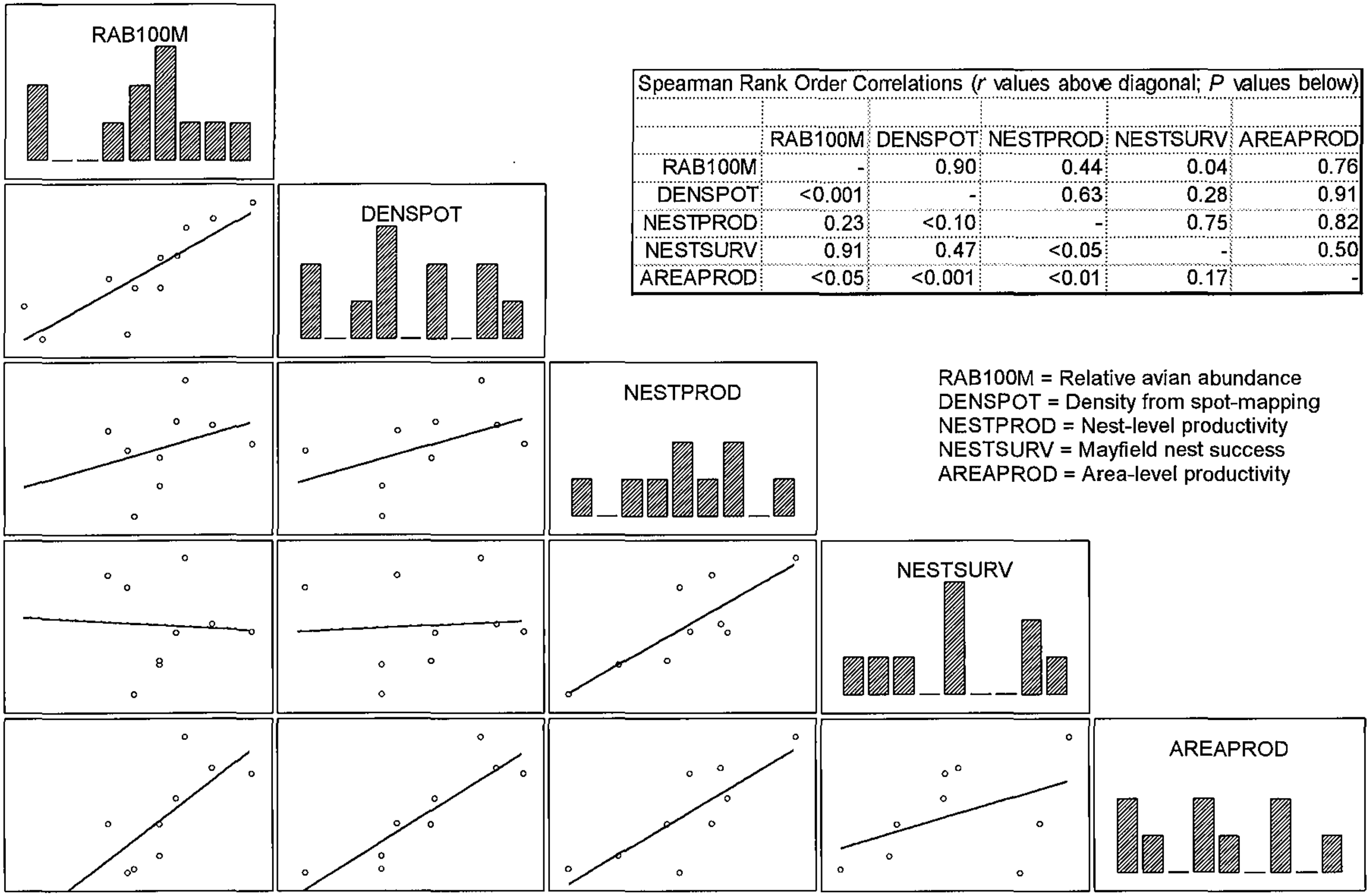


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.80	0.50	1.00	1.00
DENSPOT	0.20	-	-0.50	0.50	0.50
NESTPROD	0.67	0.67	-	0.50	0.50
NESTSURV	<0.0001	0.67	0.67	-	1.00
AREAPROD	<0.0001	0.67	0.67	<0.0001	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 8k. Correlation among relative abundance, density, and reproductive success for the Winter Wren.



Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)					
	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.90	0.44	0.04	0.76
DENSPOT	<0.001	-	0.63	0.28	0.91
NESTPROD	0.23	<0.10	-	0.75	0.82
NESTSURV	0.91	0.47	<0.05	-	0.50
AREAPROD	<0.05	<0.001	<0.01	0.17	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

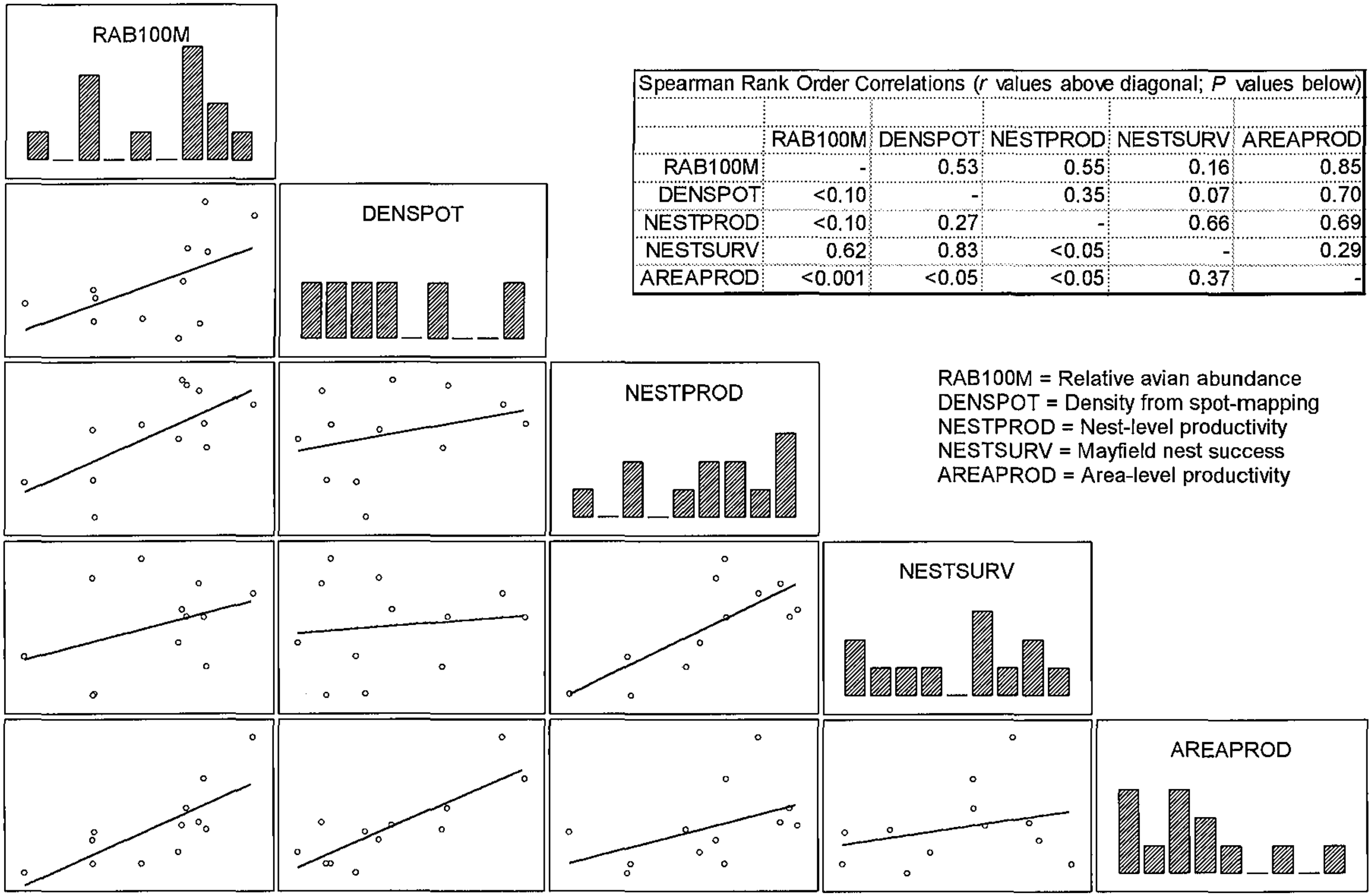
reproduction, or for species like the Song Sparrow with density independent per-capita reproduction, habitat quality can likely be inferred from measures of abundance (e.g., point-count surveys) as long as nest numbers also increase with bird numbers. This is a reliable assumption and is supported by our data. Of course in these cases, habitat quality measures are not standardized among species and can only be interpreted qualitatively.

Three species each exhibited one significant negative correlation among these variables: (1) DENSPOT vs. NESTPROD for the Chestnut-backed Chickadee (Fig. 8c) and Varied Thrush (Fig. 8i); and (2) DENSPOT vs. NESTSURV for the Pacific-slope Flycatcher (Fig. 8f). For these species, therefore, it appeared that per-capita reproductive success was density dependent. That is, the greater the density of birds, the lower the reproductive output, either in terms of fewer young fledged per nest or reduced nest survivorship. For such species with density dependent per-capita reproduction, measures of abundance from point-count surveys would not be reliable indicators of habitat quality. In fact, based upon our data, habitat quality would be highest (i.e., nest-level productivity and survivorship would be high) where abundance or density was lowest, and vice versa. Again, this conclusion holds only if nest numbers increase with bird numbers.

Analyses of data for species' guilds or groups generally yielded density independent and inversely density dependent relationships between abundance/density and per-capita reproduction (Figs. 9–12). At this level, therefore, it appears that habitat quality can again be reliably inferred from survey data. The only guild for which density dependent patterns were observed was for ground-feeding birds (Fig. 11b), where both RAB100M and DENSPOT were significantly negatively correlated with NESTSURV. For this group of birds considered collectively, therefore, we caution against relying on survey data to infer habitat quality as derived from nest-level measures of reproduction.

3.3.2. ***Correlations among abundance, density, and area-level reproduction*** - Nest-level measures of reproduction (and their correlations with abundance and density) are useful, but the best index of habitat quality is the number of young produced per unit area (not the number of young produced per nest). As discussed above (see section 3.3.4.), however, measuring area-level productivity is difficult to accomplish. Using our measure of area-level productivity (AREAPROD, defined above), we therefore re-examined correlations with abundance and density to further examine the principle objective of this study. If habitat quality can be reliably inferred from measures of abundance and/or density, we would expect positive correlations between abundance/density and area-level reproduction; if, on the other hand, abundance/density are uncorrelated, or negatively correlated, with area-level reproduction, we would question the use of survey data to reliably assess habitat

Figure 9a. Correlation among relative abundance, density, and reproductive success for resident birds.

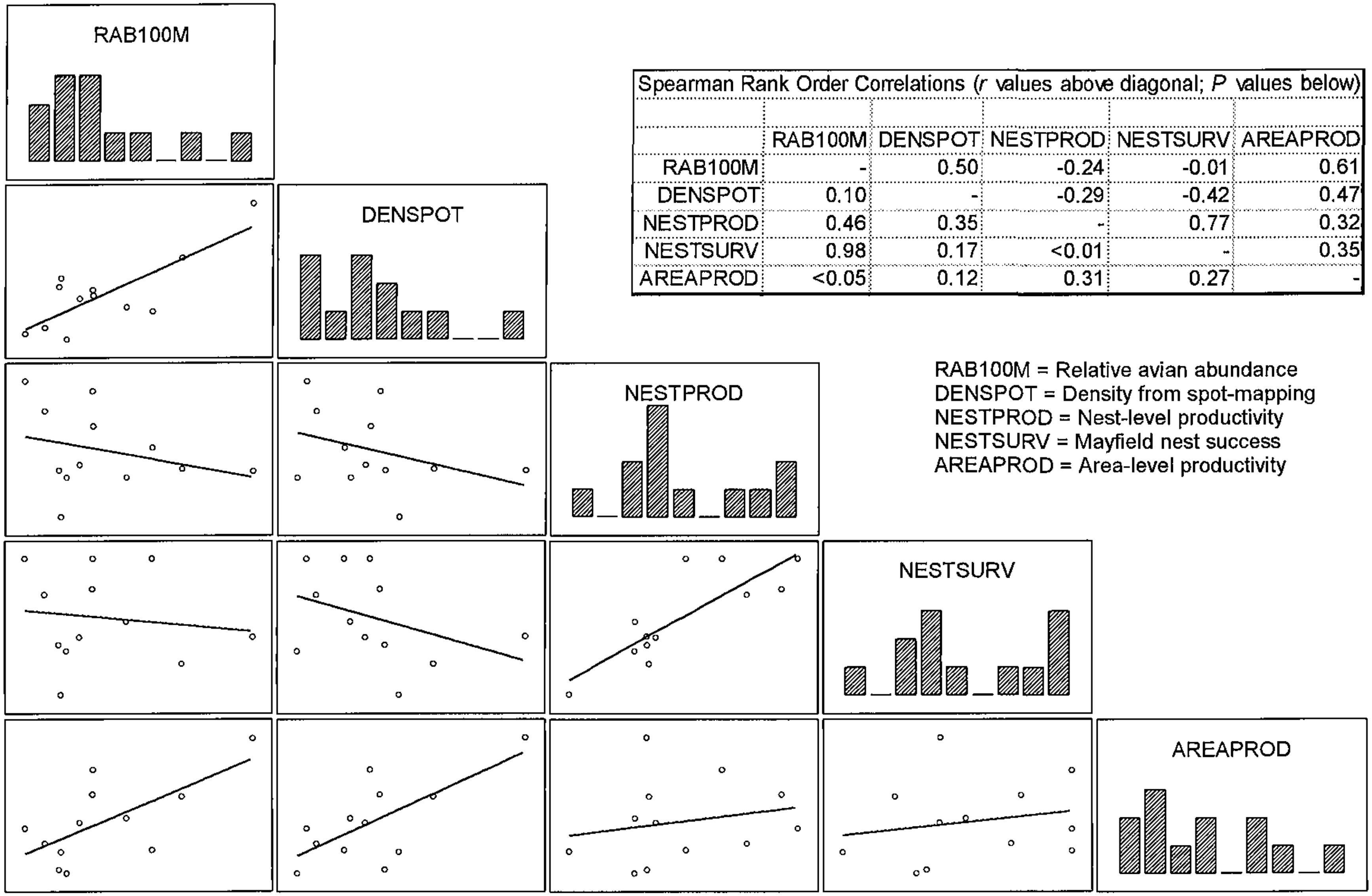


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.53	0.55	0.16	0.85
DENSPOT	<0.10	-	0.35	0.07	0.70
NESTPROD	<0.10	0.27	-	0.66	0.69
NESTSURV	0.62	0.83	<0.05	-	0.29
AREAPROD	<0.001	<0.05	<0.05	0.37	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 9b. Correlation among relative abundance, density, and reproductive success for migrant birds.

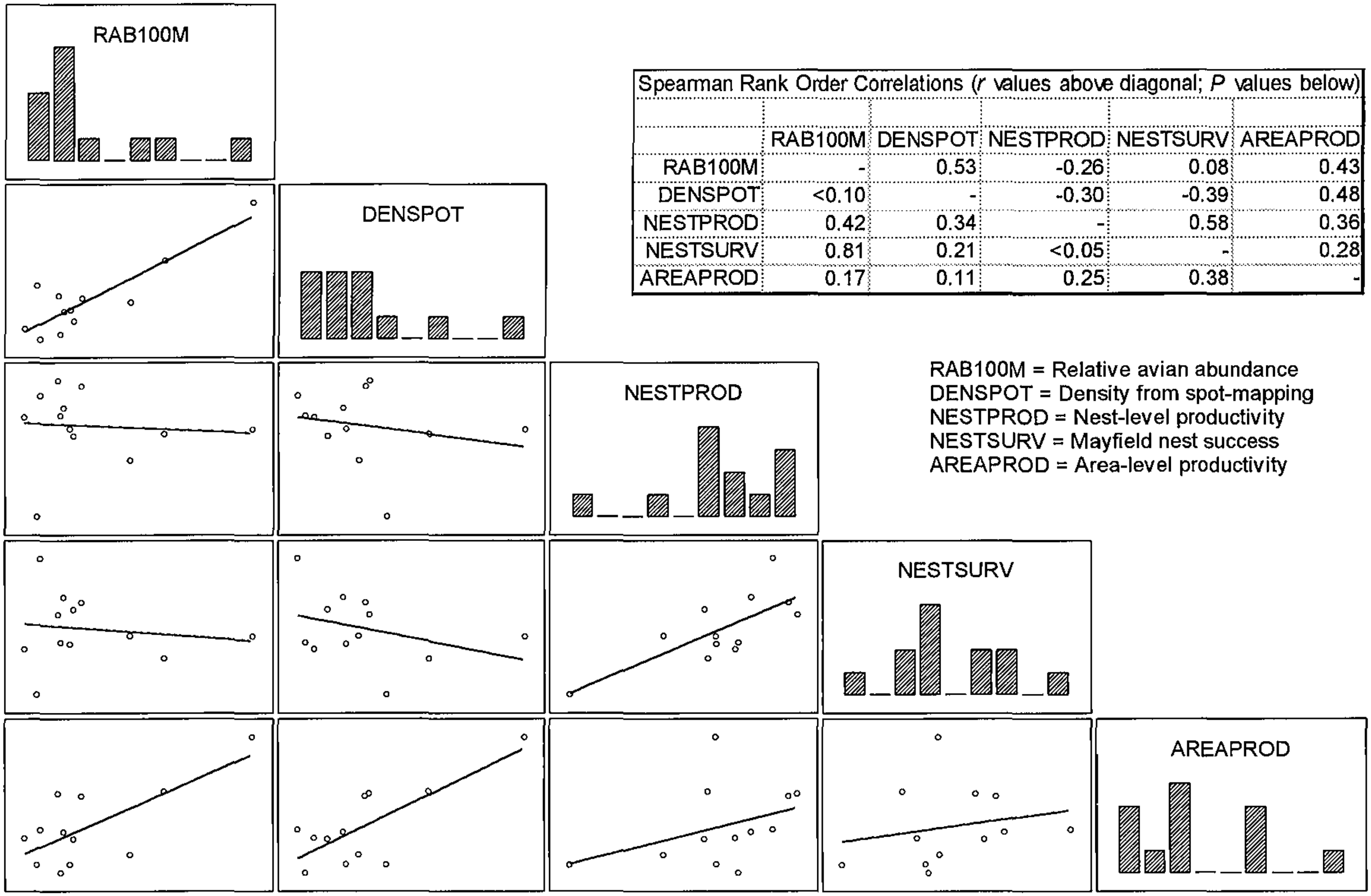


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.50	-0.24	-0.01	0.61
DENSPOT	0.10	-	-0.29	-0.42	0.47
NESTPROD	0.46	0.35	-	0.77	0.32
NESTSURV	0.98	0.17	<0.01	-	0.35
AREAPROD	<0.05	0.12	0.31	0.27	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 10a. Correlation among relative abundance, density and reproductive success for open-cup-nesting birds.

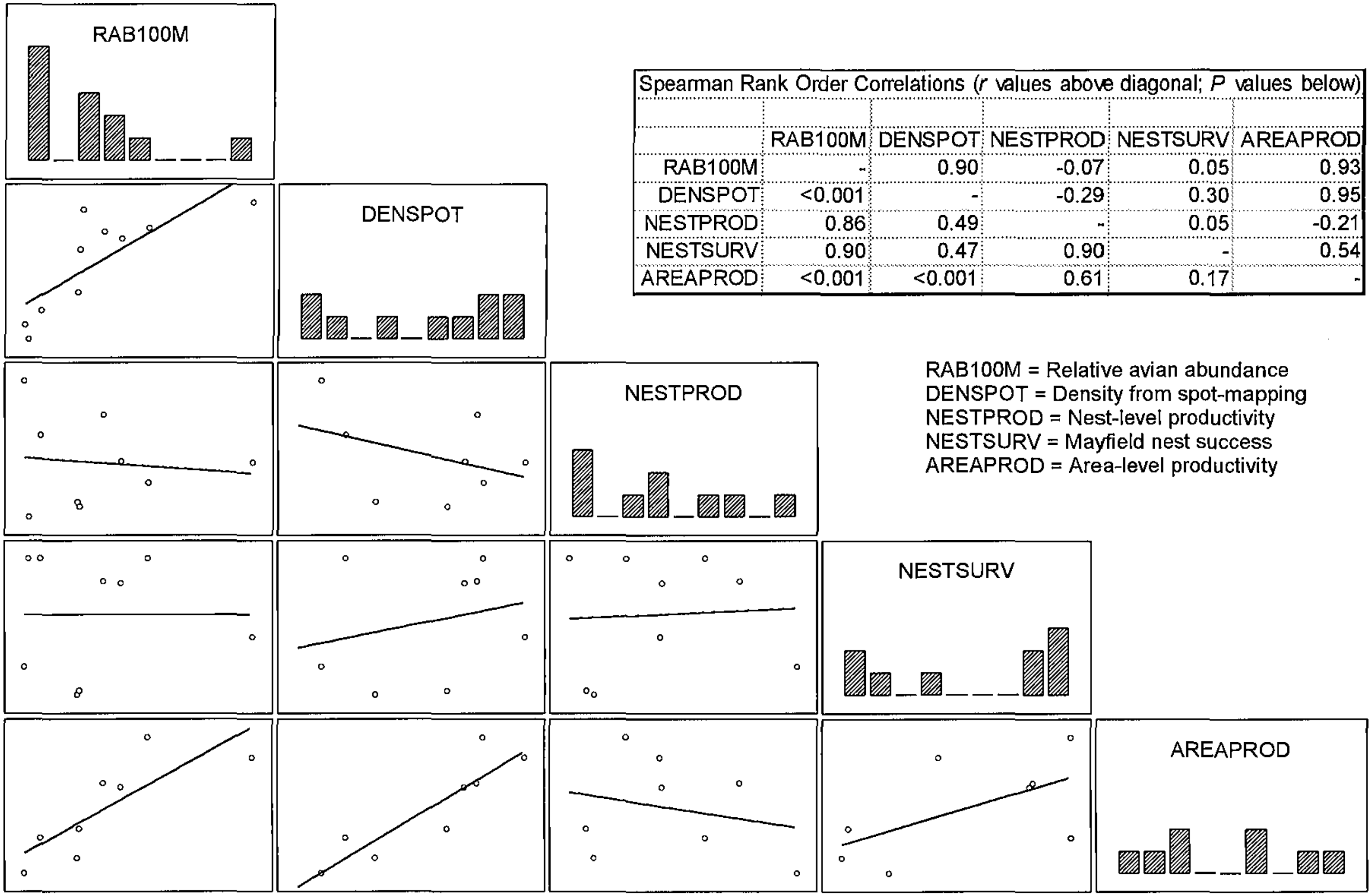


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.53	-0.26	0.08	0.43
DENSPOT	<0.10	-	-0.30	-0.39	0.48
NESTPROD	0.42	0.34	-	0.58	0.36
NESTSURV	0.81	0.21	<0.05	-	0.28
AREAPROD	0.17	0.11	0.25	0.38	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 10b. Correlation among relative abundance, density, and reproductive success for ground-nesting birds.

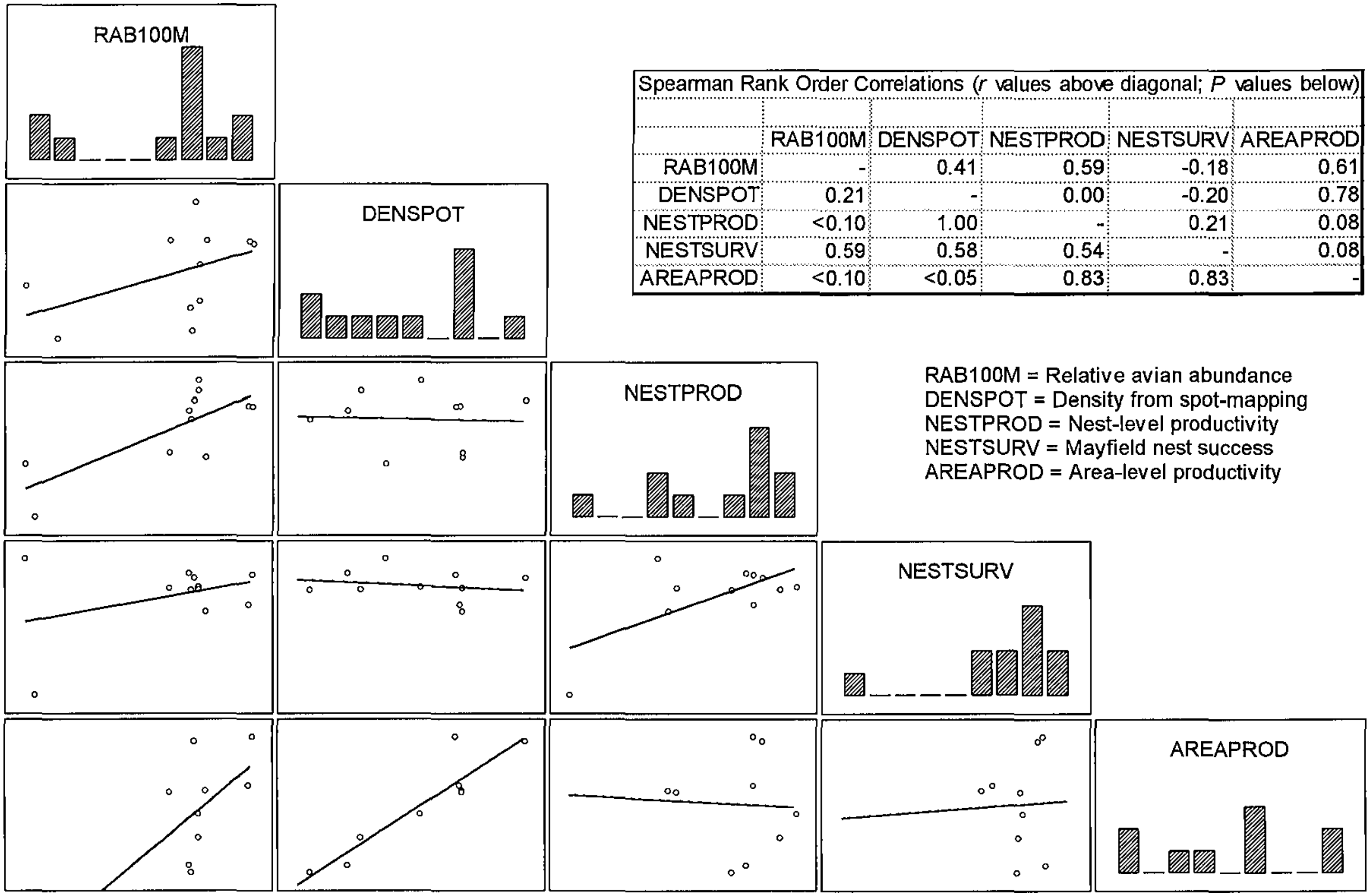


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.90	-0.07	0.05	0.93
DENSPOT	<0.001	-	-0.29	0.30	0.95
NESTPROD	0.86	0.49	-	0.05	-0.21
NESTSURV	0.90	0.47	0.90	-	0.54
AREAPROD	<0.001	<0.001	0.61	0.17	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 10c. Correlation among relative abundance, density and reproductive success for cavity-nesting birds.

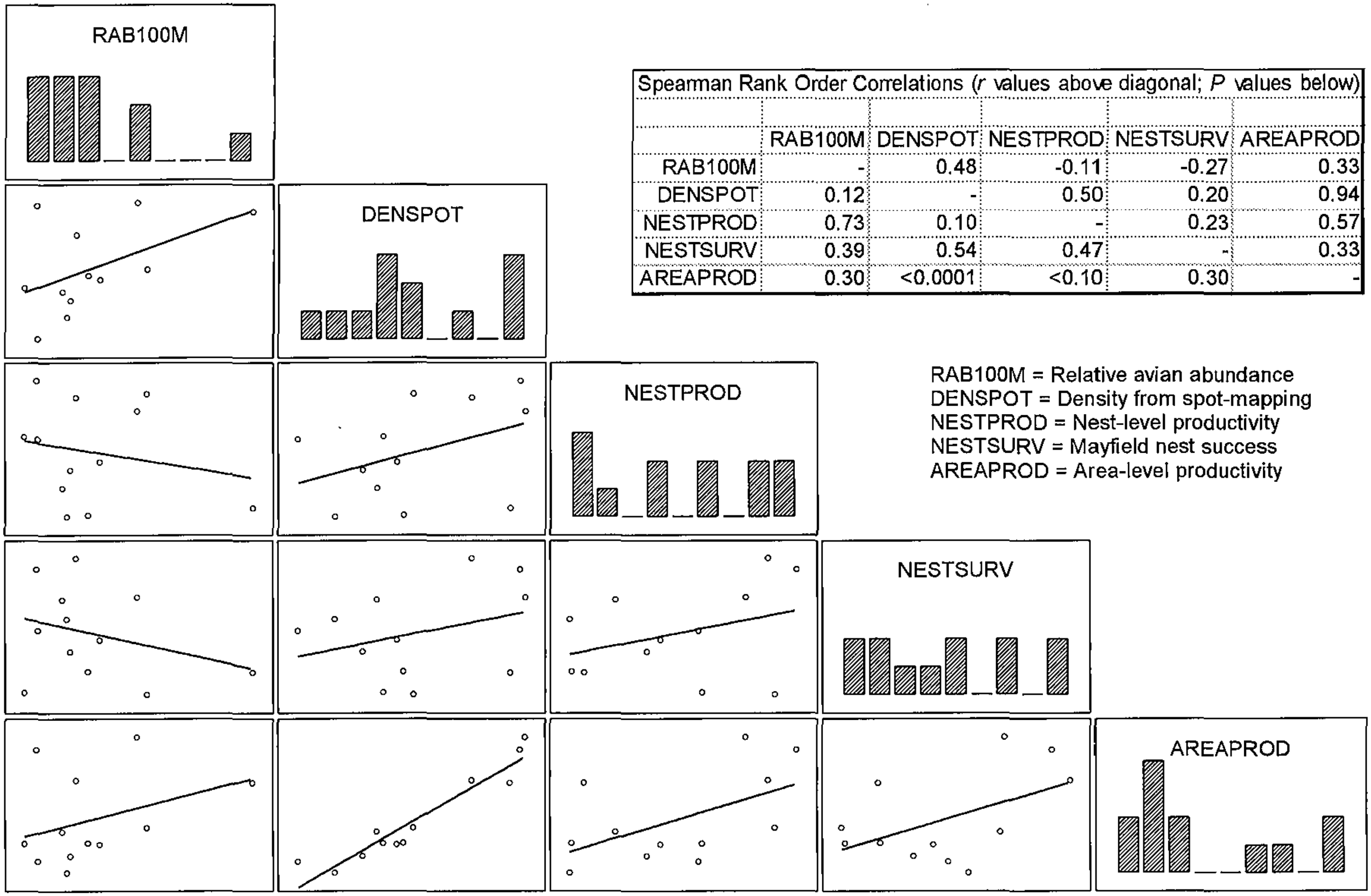


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.41	0.59	-0.18	0.61
DENSPOT	0.21	-	0.00	-0.20	0.78
NESTPROD	<0.10	1.00	-	0.21	0.08
NESTSURV	0.59	0.58	0.54	-	0.08
AREAPROD	<0.10	<0.05	0.83	0.83	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 11a. Correlation among relative abundance, density, and reproductive success for foliage-gleaning birds.

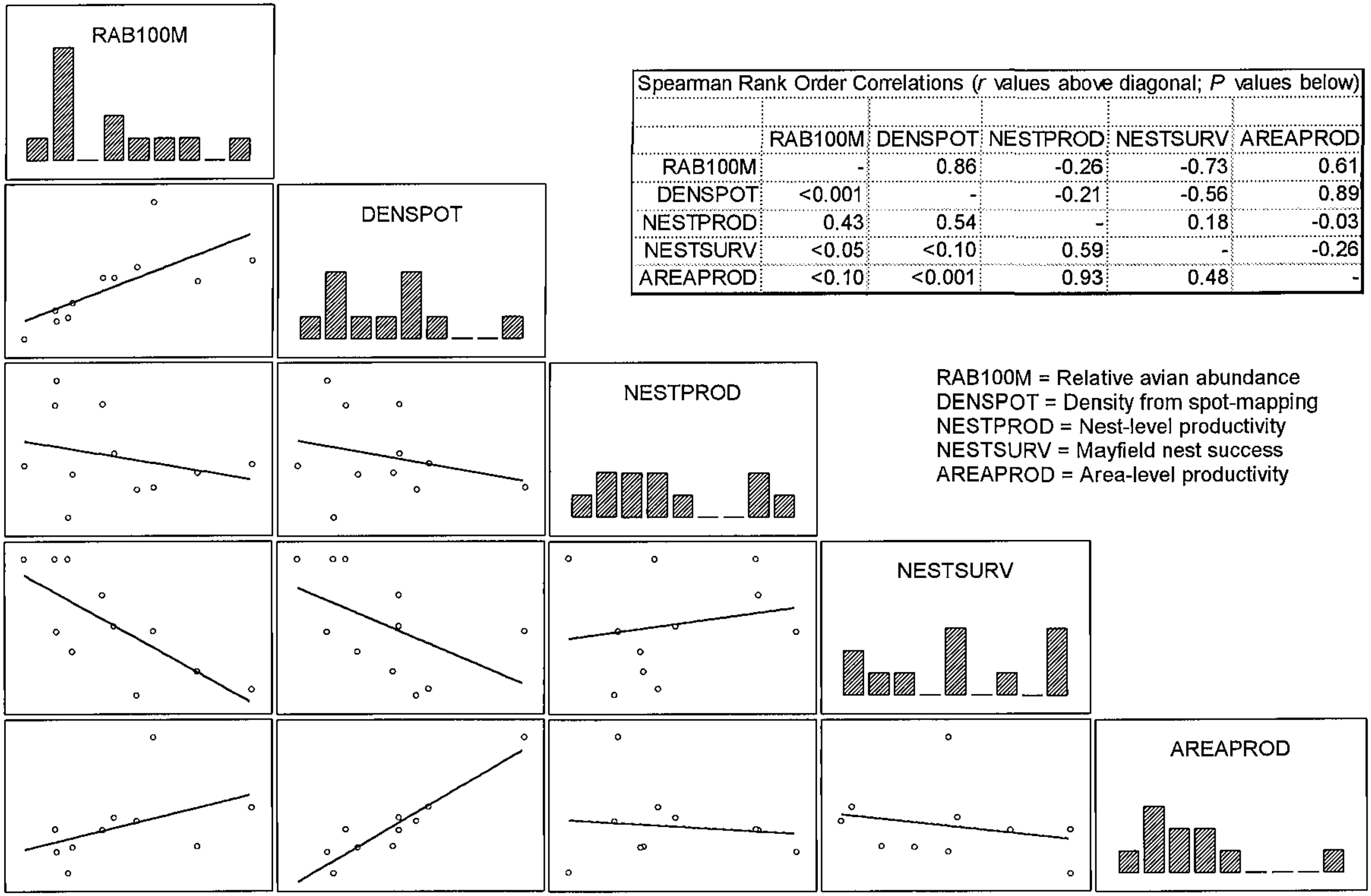


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.48	-0.11	-0.27	0.33
DENSPOT	0.12	-	0.50	0.20	0.94
NESTPROD	0.73	0.10	-	0.23	0.57
NESTSURV	0.39	0.54	0.47	-	0.33
AREAPROD	0.30	<0.0001	<0.10	0.30	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 11b. Correlation among relative abundance, density, and reproductive success for ground-feeding birds.

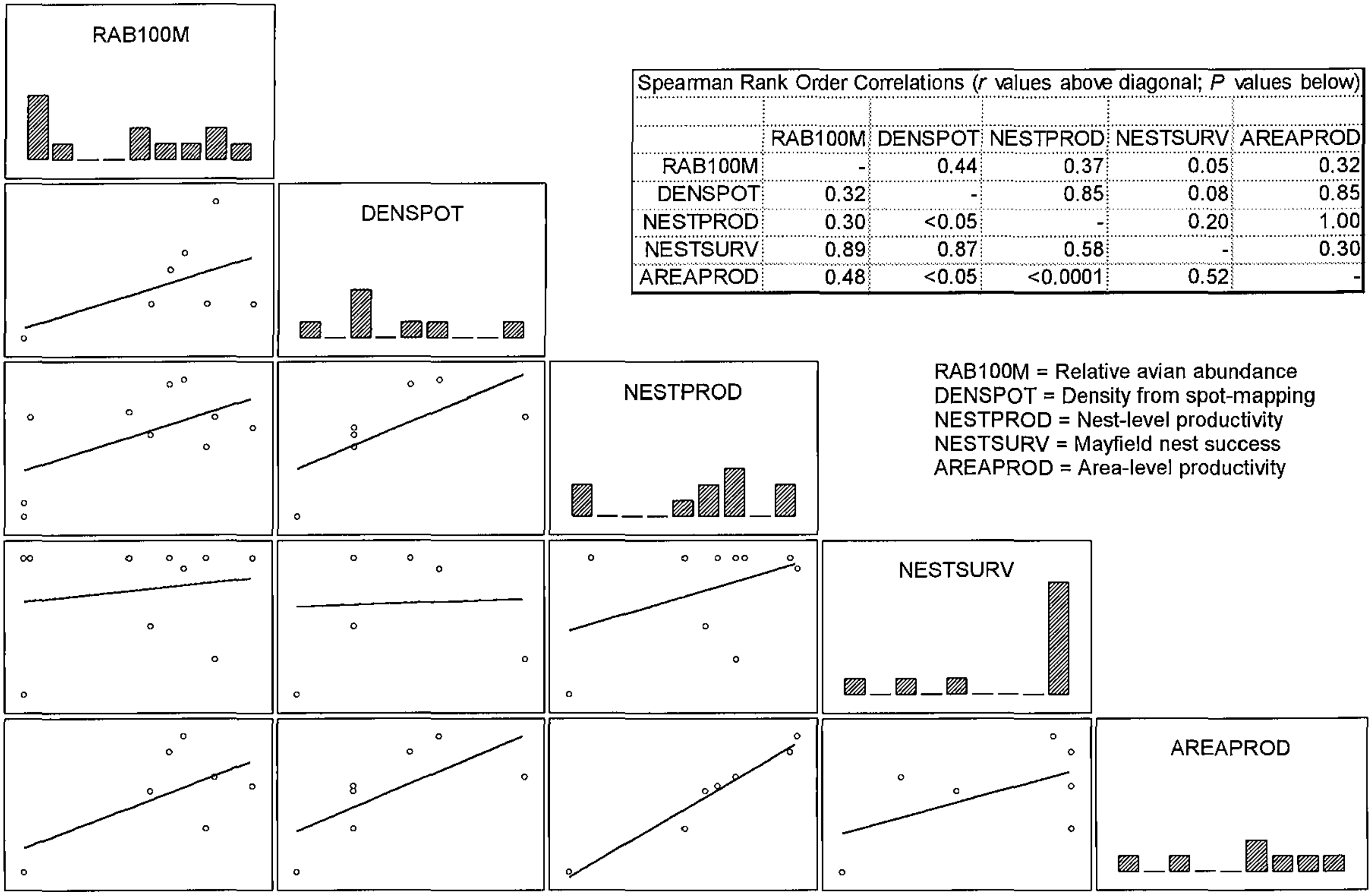


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.86	-0.26	-0.73	0.61
DENSPOT	<0.001	-	-0.21	-0.56	0.89
NESTPROD	0.43	0.54	-	0.18	-0.03
NESTSURV	<0.05	<0.10	0.59	-	-0.26
AREAPROD	<0.10	<0.001	0.93	0.48	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 11c. Correlation among relative abundance, density, and reproductive success for bark-gleaning birds.

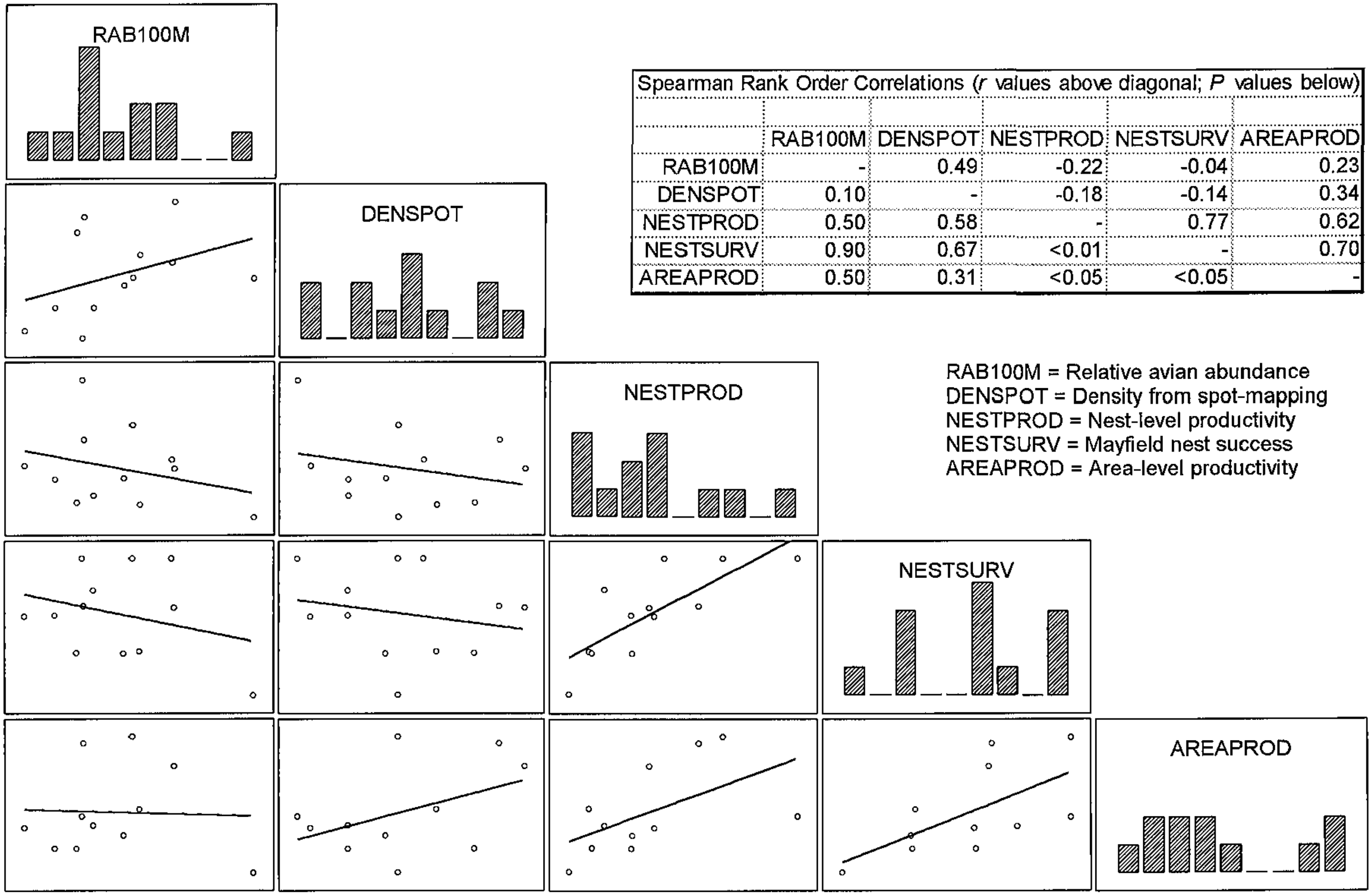


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.44	0.37	0.05	0.32
DENSPOT	0.32	-	0.85	0.08	0.85
NESTPROD	0.30	<0.05	-	0.20	1.00
NESTSURV	0.89	0.87	0.58	-	0.30
AREAPROD	0.48	<0.05	<0.0001	0.52	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 11d. Correlation among relative abundance, density, and reproductive success for aerial-feeding birds.

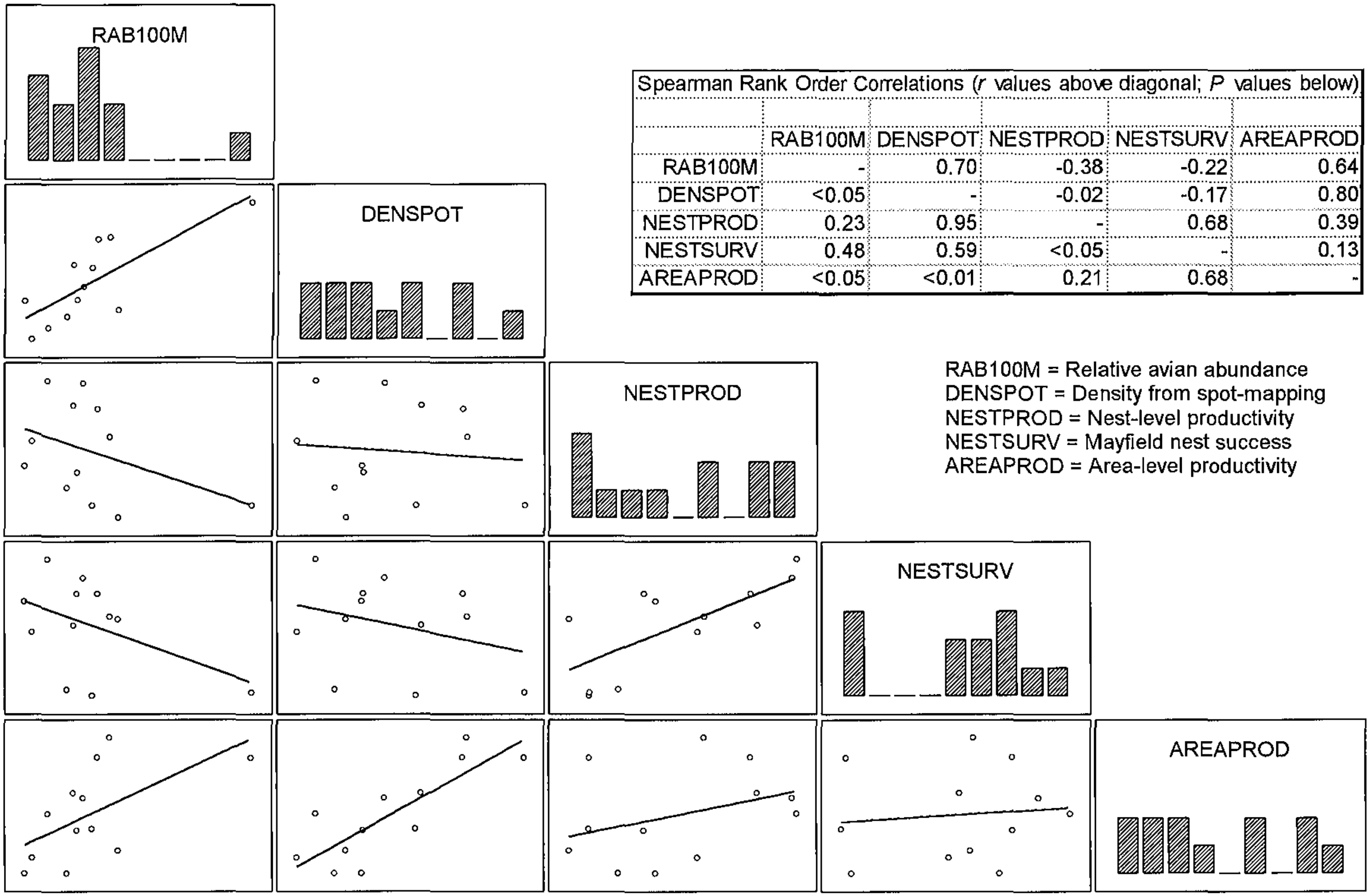


Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)

	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.49	-0.22	-0.04	0.23
DENSPOT	0.10	-	-0.18	-0.14	0.34
NESTPROD	0.50	0.58	-	0.77	0.62
NESTSURV	0.90	0.67	<0.01	-	0.70
AREAPROD	0.50	0.31	<0.05	<0.05	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

Figure 12. Correlation among relative abundance, density, and reproductive success for all breeding birds combined.



Spearman Rank Order Correlations (*r* values above diagonal; *P* values below)					
	RAB100M	DENSPOT	NESTPROD	NESTSURV	AREAPROD
RAB100M	-	0.70	-0.38	-0.22	0.64
DENSPOT	<0.05	-	-0.02	-0.17	0.80
NESTPROD	0.23	0.95	-	0.68	0.39
NESTSURV	0.48	0.59	<0.05	-	0.13
AREAPROD	<0.05	<0.01	0.21	0.68	-

RAB100M = Relative avian abundance
DENSPOT = Density from spot-mapping
NESTPROD = Nest-level productivity
NESTSURV = Mayfield nest success
AREAPROD = Area-level productivity

quality. We caution that, unlike measures of nest-level reproduction (NESTPROD and NESTSURV), which were computed directly from field data without extrapolation, our calculation of AREAPROD was based on explicit assumptions that may be invalid for some species or species' groups. It is for this reason that we consider AREAPROD separately.

Significant positive correlations were found between RAB100M and AREAPROD, or between DENSPOT and AREAPROD, for the following species: Brown Creeper (Fig. 8b), Chestnut-backed Chickadee (Fig. 8c), Dark-eyed Junco (Fig. 8d), Song Sparrow (Fig. 8g), Willow Flycatcher (Fig. 8j), and Winter Wren (Fig. 8k). For these species (six of 11 analyzed), therefore, the number of young fledged per unit area increased significantly with abundance and/or density as measured using traditional point-count survey or spot-mapping techniques, respectively. Presumably, such survey techniques can be used to reliably infer habitat quality for these species. The remaining five species (American Robin, Orange-crowned Warbler, Pacific-slope Flycatcher, Spotted Towhee, and Varied Thrush) exhibited no correlations between abundance/density and area-level reproduction. With the exception of the Pacific-slope Flycatcher (Fig. 8f) and Varied Thrush (Fig. 8i), the lack of significant correlations may be a factor of low sample size and low statistical power; many of the trends for the other species in this group are positive, but not statistically significant. Scatter diagrams for the Varied Thrush and Pacific-slope Flycatcher clearly suggest "flat-line relationships" (if not negative for the Varied Thrush), however, that are far from significant, regardless of the lack of power. Note also that these were two species for which nest-level reproduction and abundance/density were significantly negatively correlated (see above). For these species, therefore, measures of abundance and/or density were apparently unrelated to habitat quality and survey data for these species should be treated with caution. Notably, we found no significant negative correlations between AREAPROD and either RAB100M or DENSPOT for any species; such a result would have been troubling because it would have suggested that survey data were highly misleading, inferring that the lowest quality habitat was in fact the highest, and vice versa.

When individual species were combined into guilds or species' groups, we found area-level reproduction to be significantly positively correlated with abundance and/or density in the majority of cases (Figs. 9–12). In fact, only the abundance and density of aerial-feeding birds (primarily flycatchers), as a group, were uncorrelated with area-level production (Fig. 11d). With the exception of this feeding guild, therefore, our results suggest that if researchers and/or managers were interested in assessing forest quality for breeding bird communities as a whole, survey techniques like point counts and spot mapping would yield reliable data. Our finding that area-level productivity was significantly correlated with abundance and/or density for most species' groups yet uncorrelated for five of 11 individual species may indicate that sample sizes for most single species were too small to detect statistical patterns. While this may be true for some species (e.g., Orange-crowned Warbler; Fig. 8e), it does not appear to be the case for others (e.g., American Robin; Fig. 8a). Only additional data from future studies will resolve this potential sample-size problem.

To summarize these multiple comparisons for individual species and guilds or groups, we plotted the number of significant correlations (weighted by the level of significance) for each comparison among the five variables, RAB100M, DENSPOT, NESTPROD, NESTSURV, and AREAPROD (Fig. 13). Relative avian abundance and density were significantly positively correlated with area-level productivity far more frequently than with nest-level reproduction. This suggests that data from point-count and spot-mapping techniques are poor indicators of nest success as calculated using standardized nest-monitoring protocols (Martin and Geupel 1993) or the Mayfield (1975) method. As discussed above, however, the lack of positive correlations between abundance/density and nest-level reproduction does not necessarily mean that habitat quality cannot be reliably inferred using point-count and spot-mapping methodologies; as long as nest-level reproduction is not density dependent (i.e., decreases with increasing bird numbers), then common survey techniques would seem appropriate. As expected, the two measures of nest-level reproduction were more highly correlated with each other than with any other variables included in our analyses. Among all variables tested, area-level productivity was most highly correlated with bird density, perhaps because of the way we calculated AREAPROD using territory number as a surrogate for nest number (Fig. 13). Nevertheless, this result provides evidence in support of the notion that density derived from spot mapping is a better index of habitat quality compared with relative abundance derived from point counts. Although more time-consuming, therefore, our data suggest that in lieu of finding nests, researchers may better assess habitat quality by mapping territories than conducting point counts.

3.3.3. *Effects of forest treatment* - To this point in this report we have made no attempt to separate analyses by forest treatment (i.e., clearcut, commercial thin, or old growth; see Table 1). We believed the most robust way to validate the habitat quality assumption was to examine correlations between abundance and density (section 2, above), and among abundance, density, and reproduction (section 3, above), across as broad an array of forest conditions as possible. Having said this, however, we also were fully aware of the fact that researchers typically use survey techniques to compare different forest habitats or timber harvest prescriptions (reviewed by Sallabanks et al. 2001b) with respect to their "attractiveness" to birds. Hence, it is important to know if the relationship between survey data and habitat quality varies with forest treatment. For this reason, here we take further advantage of our experimental design, and where possible, compare treatment-specific relationships between abundance and

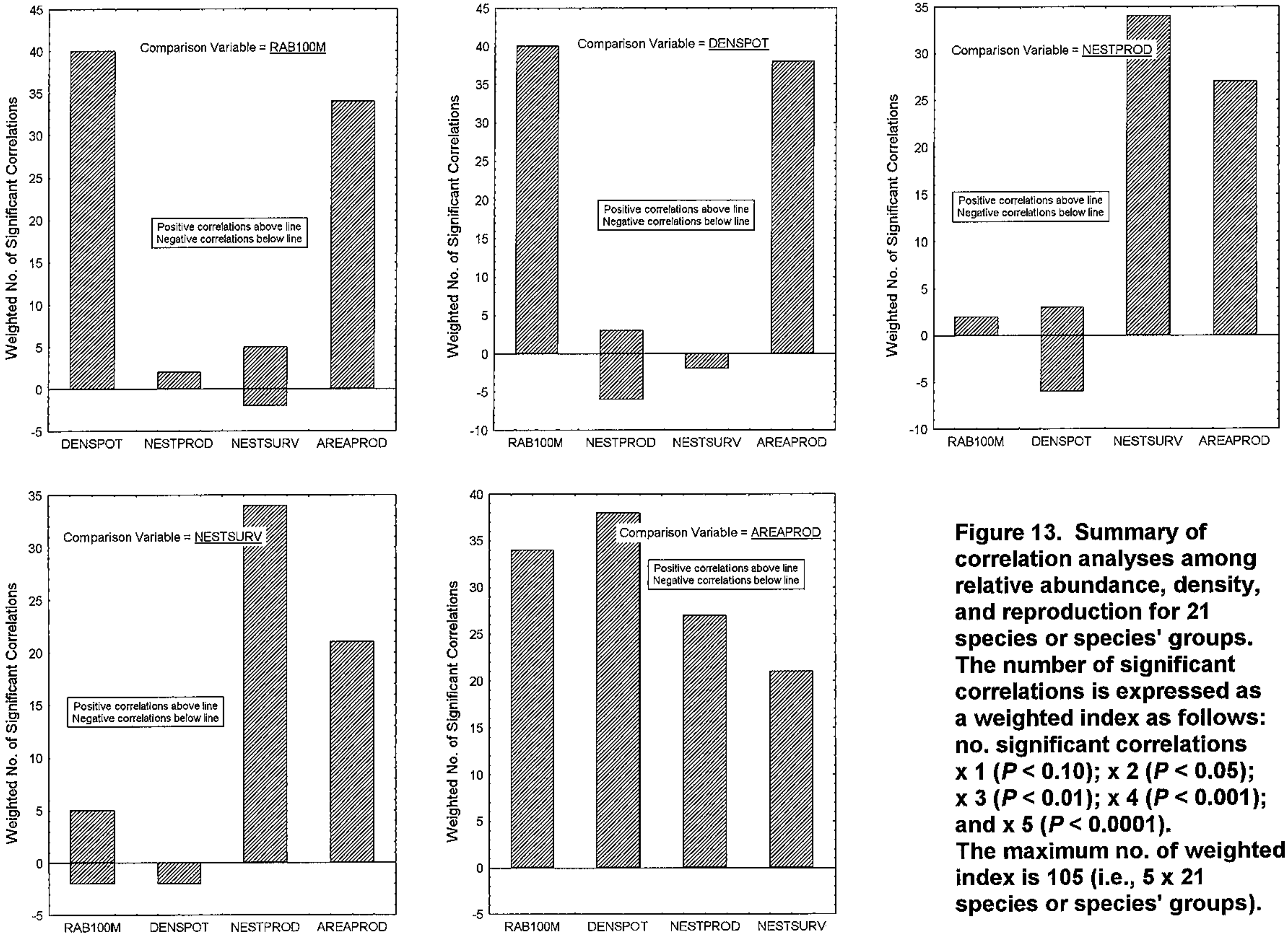


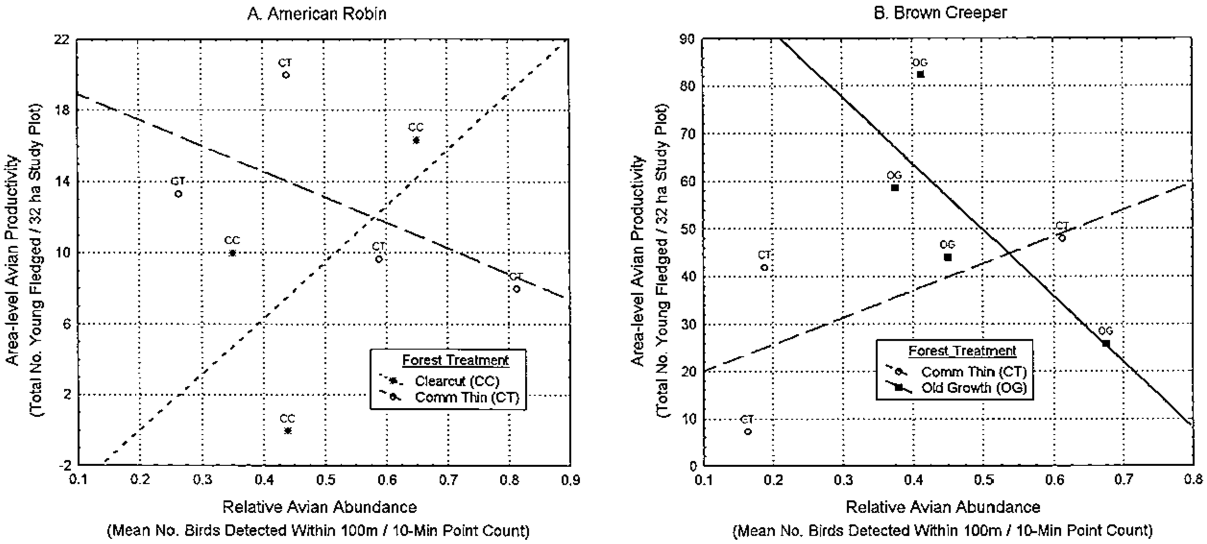
Figure 13. Summary of correlation analyses among relative abundance, density, and reproduction for 21 species or species' groups. The number of significant correlations is expressed as a weighted index as follows: no. significant correlations x 1 ($P < 0.10$); x 2 ($P < 0.05$); x 3 ($P < 0.01$); x 4 ($P < 0.001$); and x 5 ($P < 0.0001$). The maximum no. of weighted index is 105 (i.e., 5 x 21 species or species' groups).

reproductive success. Due to the high degree of correlation between relative avian abundance and density (Tables 4 and 6, Fig. 13), and because researchers use point counts far more frequently than spot mapping (Sallabanks et al. 2000a), we chose to only examine abundance (RAB100M) in treatment-level analyses. For reasons previously described, our preferred measure of reproduction was area-level productivity (AREAPROD). To examine effects of forest treatment, we generated categorized scatterplots, computed regression coefficients (slopes, *b*) separately for each treatment, and compared slopes using statistical tests.

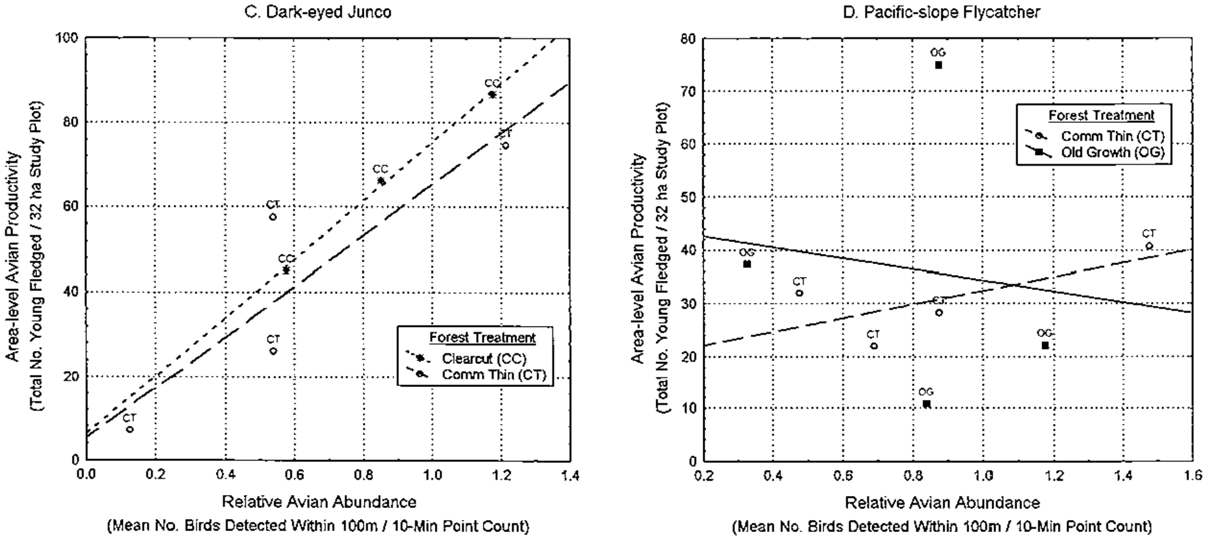
Sufficient data were obtained to perform treatment-level analyses on five bird species (Fig. 14) and all avian guilds (Figs. 15–18). No species had enough data to compare all three forest treatments. Regression coefficients and comparative statistics for all data illustrated in Figs. 14–18 are presented in Table 12. Statistically speaking, we found no differences in the relationships between abundance and area-level reproduction for any species or species' group included in analyses (Table 12). That is, slopes of regression lines for abundance vs. reproduction were not found to vary with forest treatment in any analysis. For some species or species' groups, examination of scatterplots would suggest otherwise, however. Consider, for example, data for the American Robin (Fig. 14a) and Brown Creeper (Fig. 14b). For these species, the relationship between abundance and habitat quality (as measured by area-level reproduction) appears to be different for the two forest treatments illustrated. In fact, the relationships appear to be in direct conflict with one another, suggesting that inferences about habitat quality using point-count surveys are treatment-dependent: more birds means better habitat in clearcuts for the robin and in thinned stands for the creeper, whereas more birds means worse habitat in thinned stands for the robin and in old growth for the creeper. By extension, such results imply that many birds on point counts in one forest treatment means something very different from many birds on point counts in another forest treatment. Clearly, the implications for management are enormous if these observed patterns are indeed real.

Several other comparisons, especially for feeding guilds (Fig. 17), revealed similar patterns of conflicting treatment-level relationships between abundance and reproduction. Despite the lack of statistical significance, which is possibly a sample-size issue rather than a real lack of biological significance, we urge researchers in the future to be aware of the potential for measures of abundance and density to be misleading indicators of habitat quality for some species in some habitats. This cautionary warning has been made by others (Krebs 1971, Van Horne 1983, Pulliam 1988, Robbins et al. 1989, Gibbs and Faaborg 1990, Blake 1991, Martin 1992, Vickery et al. 1992a, Hagan et al. 1996, Lautenschlager 1997) and we make it again here with data from forests of the Pacific Northwest.

The only comparison of slopes that was marginally significant was that for the Winter Wren (Fig. 14e, Table 12). While such a result may simply be an artifact of


A. American Robin

B. Brown Creeper


C. Dark-eyed Junco

D. Pacific-slope Flycatcher

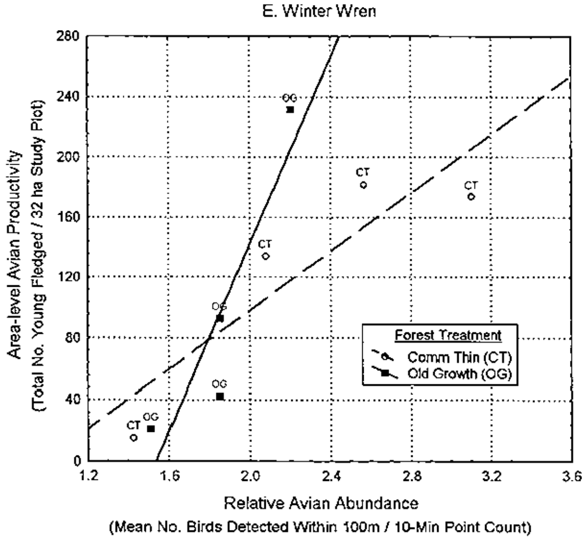
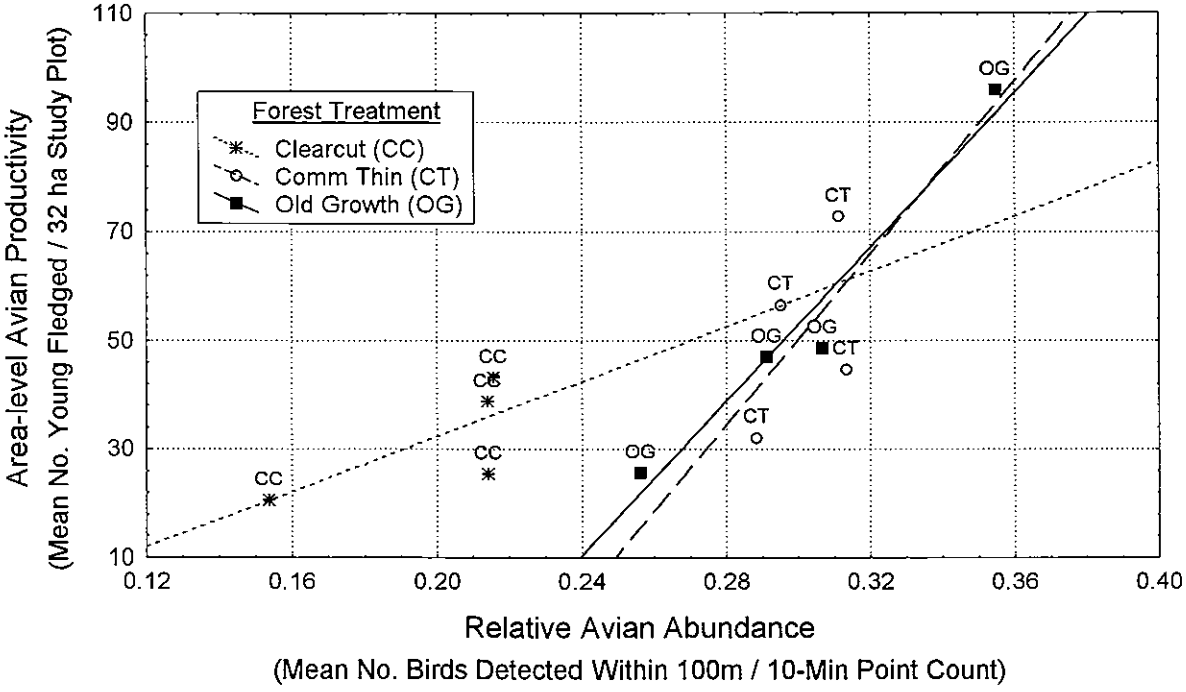

E. Winter Wren

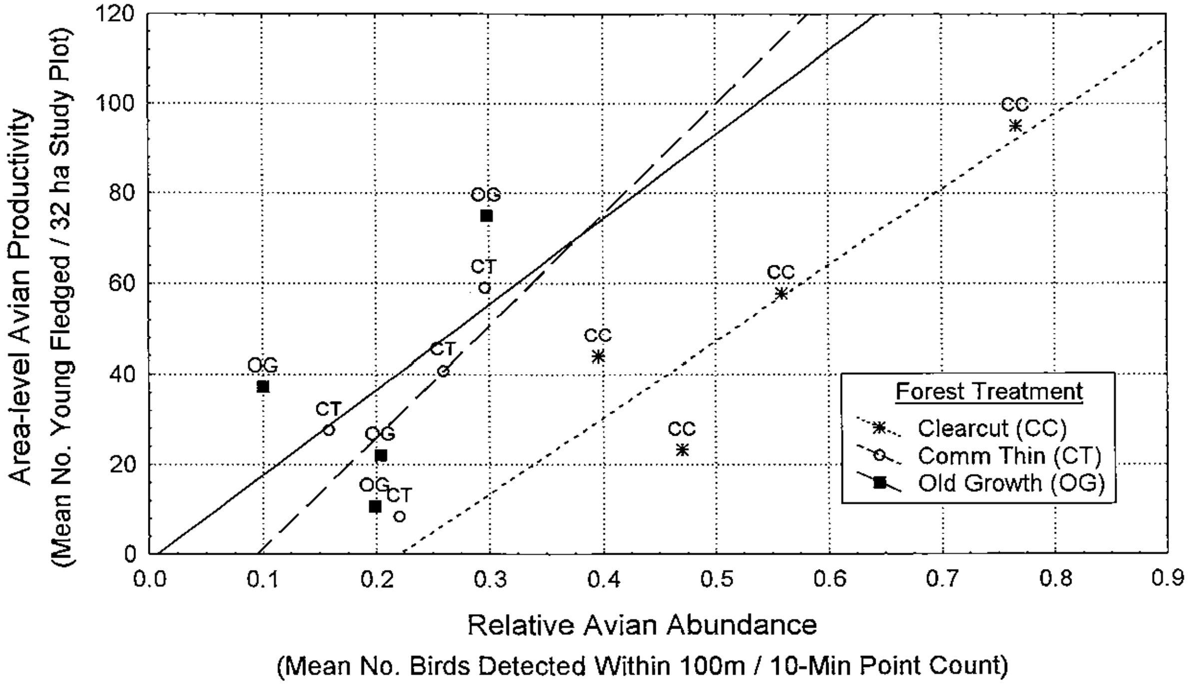
Figure 14. Scatterplots of avian abundance against area-level productivity for five species of birds with sufficient data to categorize relationships by forest treatment. See Table 12 for slope values and statistical comparisons.

Figure 15. Scatterplots of avian abundance against area-level productivity for migratory guilds, categorized by forest treatment. See Table 12 for slope values and statistical comparisons.

A. Resident Birds



B. Migrant Birds



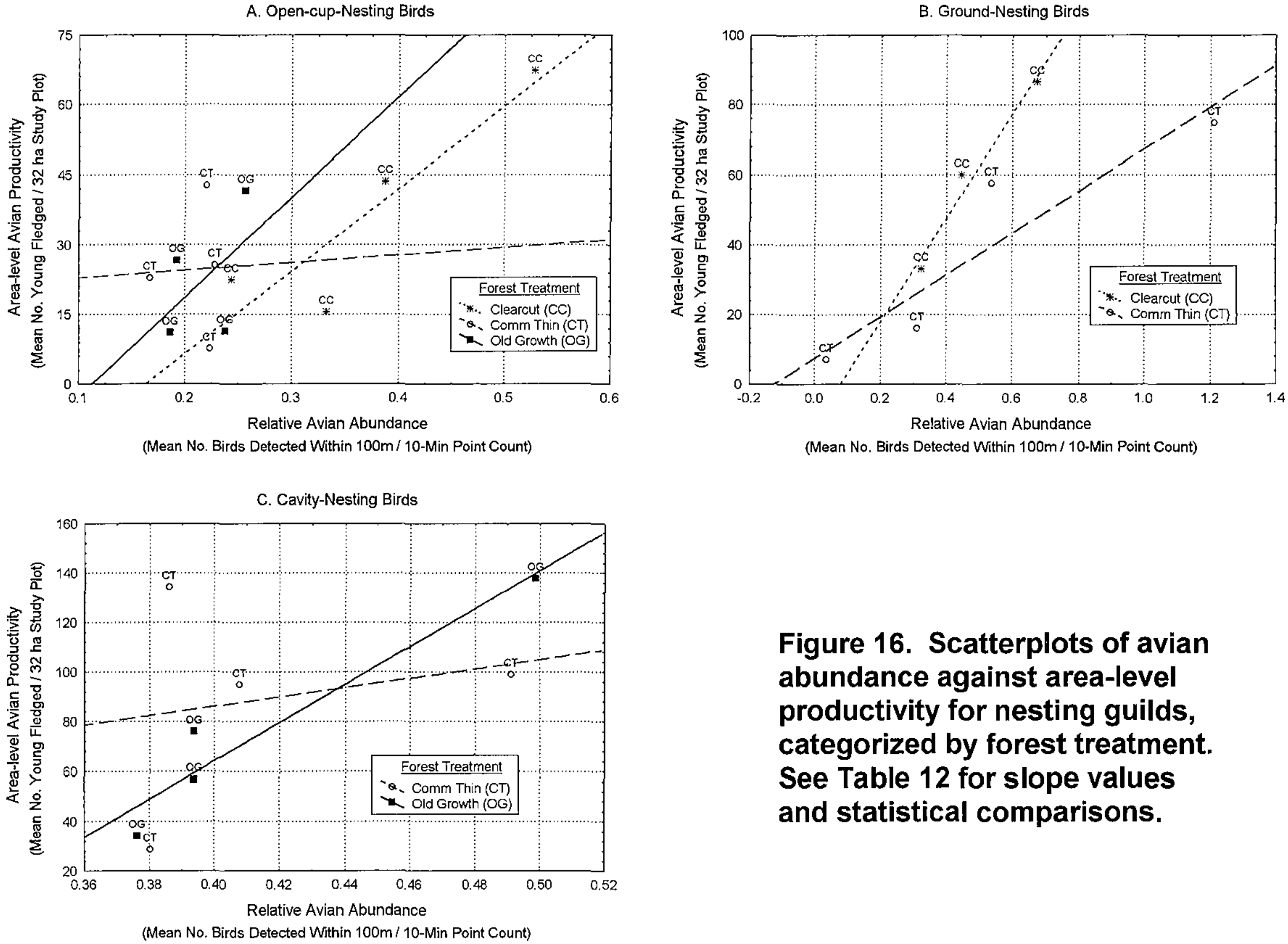


Figure 16. Scatterplots of avian abundance against area-level productivity for nesting guilds, categorized by forest treatment. See Table 12 for slope values and statistical comparisons.

Figure 17. Scatterplots of avian abundance against area-level productivity for feeding guilds, categorized by forest treatment. See Table 12 for slope values and statistical comparisons.

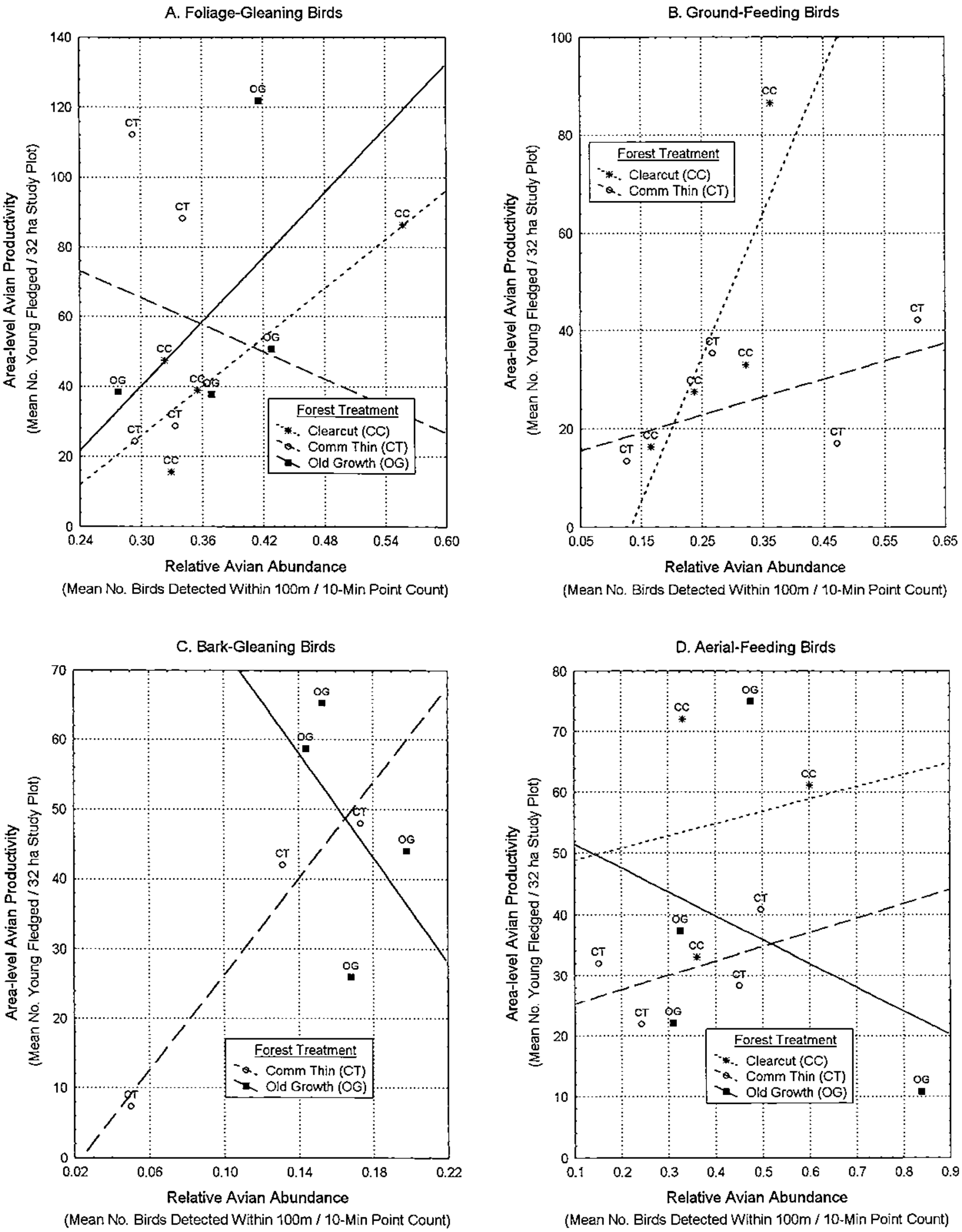


Figure 18. Scatterplot of avian abundance against area-level productivity for all bird species combined, categorized by forest treatment. See Table 12 for slope values and statistical comparisons.

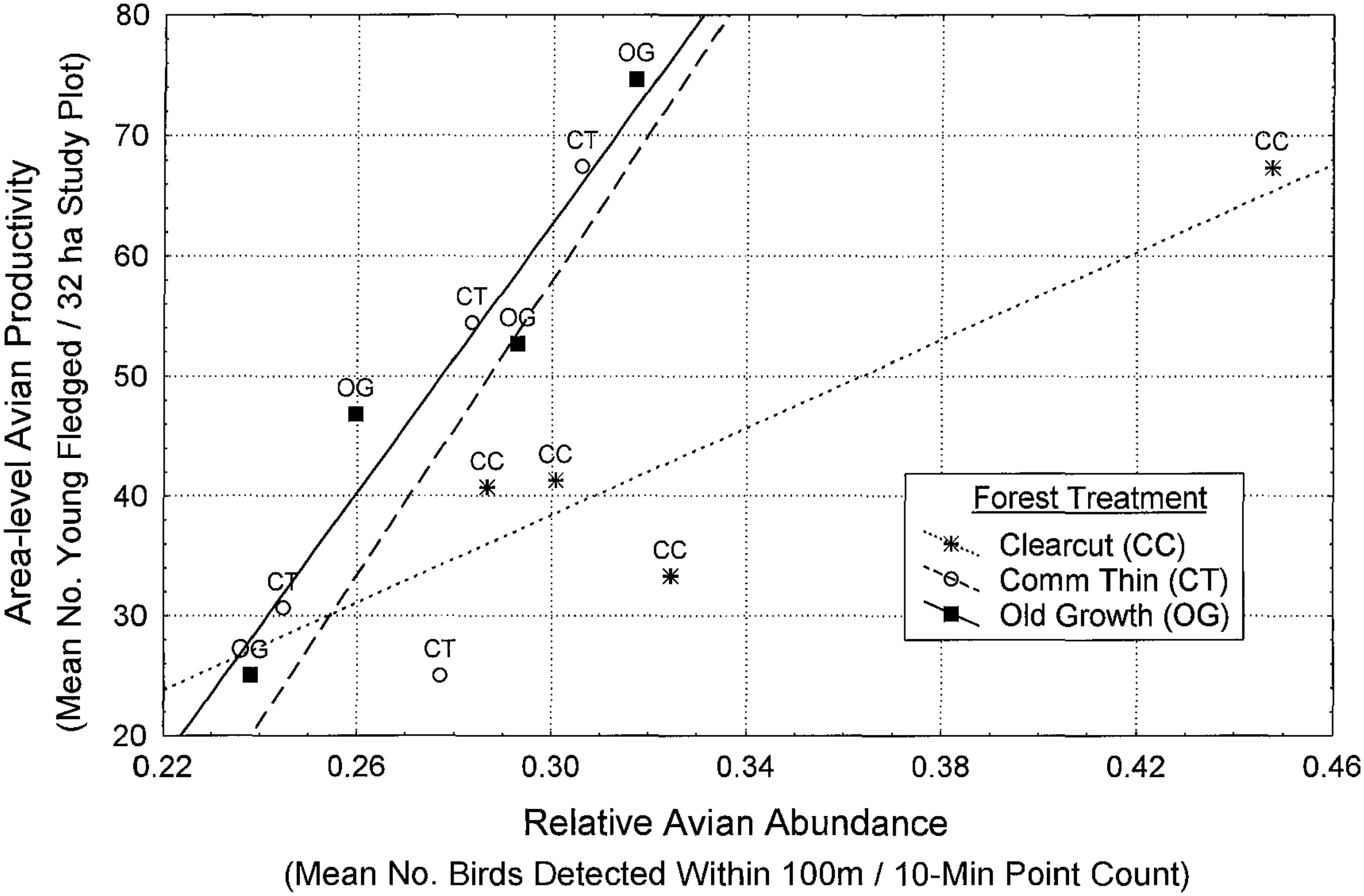


Table 12. Slope comparisons for relationships between relative avian abundance (100m point-count radius) and area-level productivity, categorized by forest treatment, for bird species and species' groups in forests of the southwest Cascade Mountains of Washington, 1998–1999.

Species or Species' Group	Slope of line, *b*, by Forest Treatment (*n*)			Test Statistic$_{(df)}$[a]	Critical Value	P[b]	Fig. No.
	Clearcut	Comm. Thin	Old Growth				
American Robin	31.19 (3)	-14.29 (4)	--	$t_3 = 1.27$	$t_{0.10(2)} = 2.35$	$0.40 < P < 0.20$	14a
Brown Creeper	--	57.63 (3)	-139.15 (4)	$t_3 = 1.96$	$t_{0.10(2)} = 2.35$	$0.20 < P < 0.10$	14b
Dark-eyed Junco	69.00 (3)	60.65 (4)	--	$t_3 = 0.22$	$t_{0.10(2)} = 2.35$	$0.90 < P < 0.50$	14c
Pacific-slope Flycatcher	--	12.95 (4)	-9.07 (4)	$t_4 = 0.42$	$t_{0.10(2)} = 2.13$	$0.90 < P < 0.50$	14d
Winter Wren	--	97.51 (4)	306.62 (4)	$t_4 = -2.13$	$t_{0.10(2)} = 2.13$	$P = 0.10$	14e
Resident Birds	260.29 (4)	1,233.55 (4)	758.45 (4)	$F_{2,6} = 2.13$	$F_{0.10(2)} = 5.14$	$0.20 < P < 0.10$	15a
Migrant Birds	168.95 (4)	249.08 (4)	188.55 (4)	$F_{2,6} = 0.06$	$F_{0.10(2)} = 5.14$	$1.00 < P < 0.75$	15b
Open-cup-Nesting Birds	173.86 (4)	45.09 (4)	200.05 (4)	$F_{2,6} = 0.08$	$F_{0.10(2)} = 5.14$	$1.00 < P < 0.75$	16a
Ground-Nesting Birds	147.84 (3)	60.15 (4)	--	$t_3 = 1.64$	$t_{0.10(2)} = 2.35$	$0.20 < P < 0.10$	16b
Cavity-Nesting Birds	--	226.35 (4)	742.27 (4)	$t_4 = -0.86$	$t_{0.10(2)} = 2.13$	$0.50 < P < 0.40$	16c
Foliage-Gleaning Birds	227.58 (4)	-68.51 (4)	314.65 (4)	$F_{2,6} = 0.09$	$F_{0.10(2)} = 5.14$	$1.00 < P < 0.75$	17a
Ground-Feeding Birds	306.66 (4)	37.42 (4)	--	$t_4 = 2.02$	$t_{0.10(2)} = 2.13$	$0.20 < P < 0.10$	17b
Bark-Gleaning Birds	--	352.84 (3)	-369.26 (4)	$t_3 = 1.97$	$t_{0.10(2)} = 2.35$	$0.20 < P < 0.10$	17c
Aerial-Feeding Birds	19.94 (3)	23.66 (4)	-38.36 (4)	$F_{2,5} = 0.23$	$F_{0.10(2)} = 5.79$	$1.00 < P < 0.75$	17d
All Species Combined	184.04 (4)	501.27 (4)	564.35 (4)	$F_{2,6} = 2.26$	$F_{0.10(2)} = 5.14$	$0.50 < P < 0.20$	18

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[a] For comparisons between two forest treatments, we used a Student's *t*-test to compare slopes; when there were sufficient data to allow comparisons among all three forest treatments, we used an *F*-test to compare slopes (Zar 1996). Because regression statistics (e.g., regression coefficients, *b*) and *t*- and *F*-tests are known to be robust with respect to deviations from normality and homoscedasticity (e.g., Jacques and Norusis 1973), we chose to use parametric tests throughout these analyses.

[b] *P*-values are given as ranges rather than exact numbers because these tests were performed by hand and critical values of test statistics were compared with observed values using standard statistical tables (Rohlf and Sokal 1981).

performing multiple statistical comparisons (where 1 in 10 tests is expected to be significant by chance alone), we consider this species worthy of further attention. To this end, we have initiated a research study focused on the Winter Wren in a subset of the same study plots on which we report here. With support from Boise State University, Washington Department of Fish and Wildlife, the U.S. Forest Service, and Weyerhaeuser Company, this study will commence in 2001 and is designed to tease apart apparent differences in breeding success and reproductive behavior of the wren between commercially-thinned and old-growth forest stands. Perhaps through this research we will also reach an understanding of why the relationships between abundance and reproduction may be habitat-dependent for the other species and species' groups alluded to in this report.

All else being equal, we conclude that previous studies that used point-count methods (with radii of ≥50 m) in western Washington (e.g., Carey et al. 1991, Gilbert and Allwine 1991, Huff and Raley 1991, Huff et al. 1991, Lundquist and Mariani 1991, Manuwal 1991, Aubrey et al. 1997) are not fatally flawed and will probably provide estimates of habitat quality for some species and most species' groups. We believe abundance estimates from other point-count studies are reasonable indicators of habitat quality to the degree that the relationship between abundance and area-level productivity is correlated, and to the degree that the shape of the abundance-productivity curves among treatments are similar. In our study, we showed that abundance was not significantly correlated with area-level productivity for approximately half of the species we analyzed. Indeed, the abundance of the Varied Thrush tended to have a negative relationship with area-level productivity (see Fig. 8i). Furthermore, and perhaps more troubling, was how forest treatment influenced the relationship between area-level productivity and abundance. Although we analyzed only a small number of species (n = 5) and relatively few replicates per treatment (n = 4), three species showed opposite trends in the relationship between abundance and area-level productivity between treatments (see Figs. 14a, b, and d); similar patterns also were found for some species' groups (see Fig. 17). This suggests that some treatments may have unique abundance-habitat quality functions for some species and species' groups that could render treatment comparisons moot. Nearly all forest-bird studies in the Pacific Northwest are intended to compare different forest treatments on a continuous scale (i.e., bird abundance is treated as a continuous variable for statistical purposes). Our study suggests that researchers may use relative avian abundance to rank the quality of forest treatments qualitatively, but that the magnitude of differences in abundance may not necessarily translate into the same magnitude of differences in habitat quality. In other words, twice as many birds on point counts in one forest treatment does not necessarily mean that one forest treatment produces twice as many young per unit area as the other. Until we know the shape of the relationship between abundance and area-level productivity (i.e., habitat quality) for specific species and habitats, we may not be able to reliably compare treatments using point-count methods.

4. Research Question #2

Based upon meta-analyses of data collected in forest types of the southwest Cascade Mountains of Washington, as well as elsewhere in the PNW, for which species (or species' guilds) is relative abundance likely to be a misleading indicator of habitat quality?

To expand our analysis beyond that already described in this report for forests of the southwest Cascade Mountains of Washington (SWWA), we pooled data with that from other geographical areas of the Pacific Northwest. We had three previous studies from which we could pool data: (1) one year (1996) of data from east-central Washington (ECWA); (2) two years (1995–1996) of data from northeast Oregon (NEOR); and (3) two years (1995–1996) of data from west-central Idaho (WCID). These three studies were all conducted in grand fir (*Abies grandis*) forests and, unlike the southwest Cascades of Washington (Westside), all were representative of the inland Pacific Northwest (Eastside) region. Originally, we also had intended to include a large data set from Idaho and Montana (Sallabanks et al. 1999) that was collected during the same years (1997–1999) as the data from the southwest Cascades of Washington; such inclusion would have more than doubled sample sizes for this meta-analysis. Unfortunately, however, data from this regional study of fragmentation were unavailable for analysis at the time of writing this report because they have not yet been published as their own independent data set for which they were originally intended.

4.1. Data Compatibility Among Studies

Combining data from different studies is less than ideal when such studies were not originally designed to complement one another. Pooling data from forests that span the entire Pacific Northwest inevitably means that some bird species (e.g., Pacific-slope Flycatcher, a primarily Westside species) will not be well represented in all regions. In addition to range differences, habitat differences also were a factor. Most limiting of all, however, is the type of data that was collected in each of the independent studies. For our meta-analyses, therefore, we were limited to comparisons of population measures that we could derive from existing field data, namely relative avian abundance and nest-level measures of reproduction. In all of the studies described above, relative avian abundance was measured using the same point-count methodology, but with 50-

m point-count radii for most studies rather than 100 m or estimated detection distances. Nest searching and monitoring also was conducted similarly among all studies. Density (from spot mapping) was not measured in any of the Eastside studies and so cannot be included in this meta-analysis. Because territories were not mapped, neither could we generate reliable estimates of area-level productivity (see Discussion in section 3.3.4.). Hence, we limit our meta-analyses to comparisons of the following three variables, all of which have been previously described: (1) relative avian abundance (number of birds detected within 50 m per 10-min point count; RAB50M); (2) nest-level productivity (mean number of young fledged per nest; NESTPROD); and (3) nest success (Mayfield estimates of nest survival; NESTSURV).

4.2. Harvest Intensity (Forest Treatment)

To analyze how forest management practices affected relationships between abundance and nest-level reproduction across the Pacific Northwest, we also assigned each forest stand to one of three "harvest intensities": (1) none (e.g., commercially mature or old-growth forest); (2) moderate (e.g., commercially thinned stands); and (3) high (e.g., clearcuts). These assignments were based upon our personal knowledge of the stand in which data were collected. We chose not to use the same categories of forest treatment as described in section 3.4.3., above, because a "clearcut" in one region was not necessarily the same as a "clearcut" in another; likewise, although all "old-growth" stands are mature forest, not all mature stands are "old-growth." The harvest intensity classification used in this meta-analysis therefore represents somewhat broader age-classes compared to that used previously in this report for the southwest Cascade Mountains of Washington. Region, forest habitat, harvest intensity, stand numbers, and years data were collected are summarized in Table 13.

4.3. Variable Computation and Data Analysis

For analyses, we selected those species or species' groups for which we had data on relative abundance (RAB50M), nest productivity (NESTPROD), and nest success (NESTSURV) in at least three study plots, regardless of geographical region. We chose three study plots as the minimum criterion by which to select species because three data points is the minimum number required to compute a correlation between two variables. In doing so, we were able to analyze data for 26 species and 10 species' groups, 6,275 individual birds, and 936 nests. We then computed mean values of abundance, nest productivity, and nest success for these species and species' groups (Table 14) as previously described for data exclusive to the southwest

Table 13. Summary of experimental design for meta-analysis comparisons between relative avian abundance and reproductive success for forest birds of the Pacific Northwest.

Pacific Northwest Region	Forest Habitat	Harvest Intensity	No. Study Plots	Year(s) Data Collected
SW Washington	Doug.-fir/ W. Hemlock	None	4	1998–1999
		Moderate	4	1998–1999
		High	4	1998–1999
EC Washington	Grand Fir	None	3	1996
		Moderate	3	1996
NE Oregon	Grand Fir	None	1	1995–1996
		Moderate	6	1995–1996
		High	1	1996
WC Idaho	Grand Fir	Moderate	5	1995–1996

Cascade Mountains of Washington (see sections 2.3 and 3.3, above). As also done before, we then screened such data for deviations from normality (Table 15). Due to significant deviations from normality in the majority of cases (Table 15), we used nonparametric Spearman rank correlation analysis to compare abundance and reproduction of forest birds across the Pacific Northwest.

4.4. Results and Discussion

4.4.1. ***Correlations between abundance and nest-level productivity*** - As found previously for data exclusive to southwest Washington, abundance and reproduction were uncorrelated for the majority of species and species' groups (Table 16). Regardless of changes in abundance, the number of young fledged per nest and the probability of nest survivorship remained constant for most species, suggesting density independent relationships between abundance and reproduction. Assuming greater nest numbers where there are more birds (an assumption supported by our own data), these results imply that where there are more birds there would be greater production

Table 14. Mean (±SE) values of relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M), nest-level productivity (mean number of young fledged per nest; NESTPROD), and nest success (Mayfield estimates of nest survival; NESTSURV) for 26 bird species and 10 species' groups from meta-analysis of data pooled from four forested regions of the Pacific Northwest.

Bird Species or Species' Group	*n*	Rel. Abundance (RAB50M)	Nest Productivity (NESTPROD)	Nest Success (NESTSURV)
Dark-eyed Junco	24	0.58 ± 0.07	2.02 ± 0.20	0.63 ± 0.08
American Robin	13	0.25 ± 0.04	1.59 ± 0.32	0.50 ± 0.12
Dusky Flycatcher	13	0.54 ± 0.12	0.68 ± 0.21	0.34 ± 0.08
Chipping Sparrow	11	0.61 ± 0.11	0.80 ± 0.34	0.45 ± 0.11
Hairy Woodpecker	9	0.07 ± 0.02	2.28 ± 0.55	0.93 ± 0.07
Red-breasted Nuthatch	9	0.37 ± 0.18	3.14 ± 0.88	1.00 ± 0.00
Swainson's Thrush	9	0.26 ± 0.06	2.03 ± 0.50	0.77 ± 0.11
Winter Wren	9	1.37 ± 0.18	2.03 ± 0.26	0.34 ± 0.07
Brown Creeper	8	0.32 ± 0.05	4.19 ± 0.53	0.75 ± 0.15
Pacific-slope Flycatcher	8	0.59 ± 0.11	2.10 ± 0.47	0.61 ± 0.13
MacGillivray's Warbler	7	0.25 ± 0.14	1.17 ± 0.61	0.26 ± 0.13
Rufous Hummingbird	7	0.23 ± 0.09	1.19 ± 0.28	0.72 ± 0.14
Warbling Vireo	7	0.24 ± 0.09	0.83 ± 0.23	0.51 ± 0.14
Chestnut-back. Chickadee	6	0.63 ± 0.05	4.50 ± 0.73	0.96 ± 0.04
Song Sparrow	6	0.71 ± 0.33	2.26 ± 0.30	0.70 ± 0.15
Varied Thrush	6	0.18 ± 0.02	1.60 ± 0.43	0.61 ± 0.19
Mountain Chickadee	5	0.49 ± 0.14	0.90 ± 0.24	1.00 ± 0.00
Northern Flicker	5	0.04 ± 0.01	3.40 ± 0.89	1.00 ± 0.00
Spotted Towhee	5	0.52 ± 0.15	0.80 ± 0.49	0.27 ± 0.12
Western Tanager	5	0.33 ± 0.07	1.95 ± 0.85	0.84 ± 0.16
Wilson's Warbler	5	0.18 ± 0.03	2.40 ± 1.03	0.70 ± 0.19
Black-headed Grosbeak	4	0.19 ± 0.03	0.54 ± 0.31	0.30 ± 0.08
Townsend's Solitaire	4	0.03 ± 0.02	0.25 ± 0.25	0.36 ± 0.22
House Wren	3	0.01 ± 0.01	1.33 ± 0.33	0.78 ± 0.22
Orange-crowned Warbler	3	0.42 ± 0.20	1.67 ± 1.01	0.48 ± 0.28
Willow Flycatcher	3	1.05 ± 0.32	2.14 ± 0.16	0.67 ± 0.06
Resident Birds	28	0.49 ± 0.04	1.98 ± 0.20	0.67 ± 0.05
Migrant Birds	26	0.39 ± 0.05	1.48 ± 0.22	0.56 ± 0.06
Open-cup-Nesting Birds	26	0.39 ± 0.06	1.33 ± 0.17	0.52 ± 0.05
Ground-Nesting Birds	24	0.53 ± 0.07	1.88 ± 0.21	0.61 ± 0.08
Cavity-Nesting Birds	19	0.42 ± 0.06	2.23 ± 0.36	0.87 ± 0.03
Foliage-Gleaning Birds	26	0.47 ± 0.06	1.62 ± 0.22	0.58 ± 0.04
Ground-Feeding Birds	26	0.46 ± 0.06	1.78 ± 0.18	0.60 ± 0.07
Bark-Feeding Birds	16	0.25 ± 0.09	2.74 ± 0.47	0.94 ± 0.03
Aerial-Feeding Birds	25	0.55 ± 0.08	1.22 ± 0.20	0.49 ± 0.07
All Species Combined	29	0.45 ± 0.04	1.71 ± 0.17	0.61 ± 0.04

Table 15. Results of Shapiro-Wilks' W tests for normal distribution of variables: relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M), nest productivity (mean number of young fledged per nest; NESTPROD), and nest success (Mayfield estimates of nest survival; NESTSURV).

Bird Species		RAB50M		NESTPROD		NESTSURV	
or Species' Group	*n*	*W*	*P*	*W*	*P*	*W*	*P*
Dark-eyed Junco	24	0.94	0.20	0.95	0.23	0.82	<0.001
American Robin	13	0.96	0.76	0.96	0.80	0.83	<0.05
Dusky Flycatcher	13	0.89	0.10	0.84	<0.05	0.91	0.17
Chipping Sparrow	11	0.83	<0.05	0.75	<0.01	0.82	<0.05
Hairy Woodpecker	9	0.87	0.13	0.87	0.14	0.39	<0.0001
Red-breasted Nuthatch	9	0.68	<0.001	0.82	<0.05	---	---
Swainson's Thrush	9	0.94	0.58	0.95	0.71	0.75	<0.01
Winter Wren	9	0.92	0.43	0.97	0.91	0.96	0.83
Brown Creeper	8	0.88	0.19	0.85	0.11	0.64	<0.001
Pacific-slope Flycatcher	8	0.95	0.75	0.90	0.27	0.88	0.19
MacGillivray's Warbler	7	0.70	<0.01	0.78	<0.05	0.76	<0.05
Rufous Hummingbird	7	0.86	0.17	0.92	0.49	0.74	<0.01
Warbling Vireo	7	0.75	<0.05	0.83	<0.10	0.87	0.17
Chestnut-back. Chickadee	6	0.84	0.12	0.93	0.58	0.50	<0.0001
Song Sparrow	6	0.84	0.14	0.90	0.35	0.83	<0.10
Varied Thrush	6	0.89	0.33	0.99	0.98	0.80	<0.10
Mountain Chickadee	5	0.70	<0.01	0.83	0.14	---	---
Northern Flicker	5	0.89	0.36	0.92	0.55	---	---
Spotted Towhee	5	0.95	0.74	0.68	<0.01	0.88	0.29
Western Tanager	5	0.80	<0.10	0.78	<0.10	0.55	<0.001
Wilson's Warbler	5	0.96	0.77	0.87	0.26	0.75	<0.05
Black-headed Grosbeak	4	0.88	0.33	0.78	<0.10	0.68	<0.01
Townsend's Solitaire	4	0.81	0.13	0.63	<0.01	0.80	<0.10
House Wren	3	0.75	<0.0001	0.75	<0.0001	0.75	<0.001
Orange-crowned Warbler	3	1.00	0.95	0.99	0.84	0.99	0.79
Willow Flycatcher	3	0.92	0.46	0.89	0.35	0.94	0.51
Resident Birds	28	0.96	0.42	0.92	<0.05	0.91	<0.05
Migrant Birds	26	0.89	<0.01	0.95	0.19	0.94	0.16
Open-cup-Nesting Birds	26	0.86	<0.01	0.96	0.46	0.97	0.53
Ground-Nesting Birds	24	0.93	<0.10	0.91	<0.05	0.80	<0.001
Cavity-Nesting Birds	19	0.98	0.90	0.91	<0.10	0.82	<0.01
Foliage-Gleaning Birds	26	0.89	<0.05	0.95	0.23	0.97	0.71
Ground-Feeding Birds	26	0.92	<0.05	0.91	<0.05	0.83	<0.001
Bark-Feeding Birds	16	0.60	<0.0001	0.91	0.12	0.55	<0.0001
Aerial-Feeding Birds	25	0.95	0.24	0.93	<0.10	0.93	<0.10
All Species Combined	29	0.78	<0.0001	0.94	<0.10	0.96	0.38

Table 16. Spearman rank correlation analysis between relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M) and nest productivity (mean number of young fledged per nest; NESTPROD), and between relative avian abundance and nest success (Mayfield estimates of nest survival; NESTSURV) for 26 species and 10 species' groups included in Pacific Northwest forests meta-analysis.

Bird Species or Species' Group		RAB50M vs. NESTPROD			RAB50M vs. NESTSURV		
	n	*r*	*t*	*P*	*r*	*t*	*P*
Dark-eyed Junco	24	0.12	0.57	0.57	-0.03	-0.15	0.89
American Robin	13	0.02	0.05	0.96	-0.07	-0.22	0.83
Dusky Flycatcher	13	0.37	1.33	0.21	0.19	0.63	0.54
Chipping Sparrow	11	-0.16	-0.48	0.64	-0.30	-0.96	0.36
Hairy Woodpecker	9	0.34	0.95	0.37	-0.35	-0.97	0.36
Red-breasted Nuthatch	9	-0.83	-3.96	<0.01	---	---	---
Swainson's Thrush	9	-0.58	-1.88	0.10	-0.20	-0.54	0.60
Winter Wren	9	0.44	1.31	0.23	0.06	0.16	0.88
Brown Creeper	8	0.06	0.15	0.89	-0.05	-0.13	0.90
Pacific-slope Flycatcher	8	-0.52	-1.51	0.18	-0.66	-2.14	<0.10
MacGillivray's Warbler	7	-0.13	-0.29	0.78	-0.22	-0.50	0.64
Rufous Hummingbird	7	0.44	1.08	0.33	0.61	1.72	0.15
Warbling Vireo	7	-0.76	-2.65	<0.05	0.04	0.08	0.94
Chestnut-back. Chickadee	6	0.46	1.05	0.35	-0.39	-0.85	0.44
Song Sparrow	6	0.50	1.15	0.31	-0.09	-0.19	0.96
Varied Thrush	6	-0.46	-1.05	0.35	-0.28	-0.58	0.59
Mountain Chickadee	5	-0.45	-0.87	0.45	---	---	---
Northern Flicker	5	-0.72	-1.79	0.17	---	---	---
Spotted Towhee	5	0.29	0.52	0.64	-0.10	-0.17	0.87
Western Tanager	5	-0.87	-3.09	<0.10	0.00	0.00	1.00
Wilson's Warbler	5	-0.56	-1.18	0.32	-0.11	-0.19	0.86
Black-headed Grosbeak	4	0.95	4.24	<0.10	0.40	0.62	0.60
Townsend's Solitaire	4	0.27	0.40	0.73	0.21	0.30	0.79
House Wren	3	1.00	---	<0.001	0.50	0.58	0.67
Orange-crowned Warbler	3	0.50	0.58	0.67	0.50	0.58	0.67
Willow Flycatcher	3	0.50	0.58	0.67	1.00	---	<0.0001
Resident Birds	28	0.00	0.00	1.00	-0.14	-0.74	0.45
Migrant Birds	26	-0.10	-0.51	0.62	-0.17	-0.86	0.40
Open-cup-Nesting Birds	26	-0.20	-1.02	0.32	-0.32	-1.63	0.12
Ground-Nesting Birds	24	0.19	0.92	0.37	-0.02	-0.07	0.94
Cavity-Nesting Birds	19	0.41	1.83	<0.10	-0.67	-3.75	<0.01
Foliage-Gleaning Birds	26	0.33	1.71	0.10	-0.14	-0.71	0.49
Ground-Feeding Birds	26	-0.04	-0.21	0.86	-0.32	-1.65	0.11
Bark-Feeding Birds	16	0.10	0.38	0.71	0.02	0.06	0.95
Aerial-Feeding Birds	25	0.13	0.60	0.55	0.01	0.05	0.96
All Species Combined	29	-0.18	-0.95	0.35	-0.29	-1.56	0.13

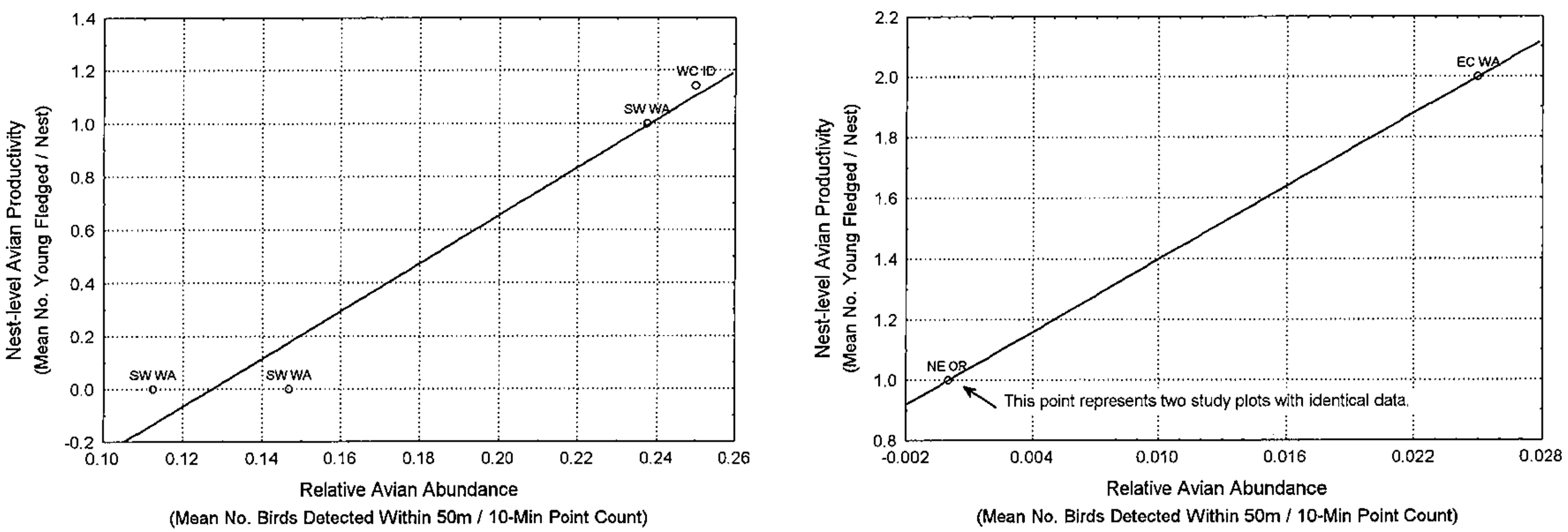
of young. Hence, for those species where nest-level reproduction is density independent, we conclude that survey data would be reliable indicators of habitat quality.

Abundance and nest-level reproduction were significantly positively correlated for three bird species (Black-headed Grosbeak, House Wren [*Troglodytes aedon*], and Willow Flycatcher; Table 16, Fig. 19). Such inverse density dependence also suggests that point-count surveys would be suitable sampling techniques with which to measure habitat quality for these species. It is for species for which we found significant negative correlations between abundance and reproduction across forests of the Pacific Northwest that we question the validity of using standardized survey techniques. In our analyses, these species were the Red-breasted Nuthatch, Warbling Vireo, Western Tanager, and Pacific-slope Flycatcher (Table 16, Fig. 20).

Somewhat paradoxically, the abundance of cavity-nesting birds was significantly positively correlated with nest-level productivity ($P < 0.10$), but significantly negatively correlated with nest success ($P < 0.01$; Table 16). In this case, given that the level of significance was an order of magnitude higher for the negative relationship with nest success, we also consider cavity-nesters as potential "problem species" when it comes to assessing habitat quality using point-count surveys. This result perhaps serves as an important reminder of how point-count surveys are primarily limited to songbirds in terms of their usefulness as a field-sampling technique for forest avifauna. The cavity-nesting birds in our analyses were primarily woodpeckers, species not well suited for detection by point counts that rely heavily on vocalizations to distinguish among species.

4.4.2. *Effects of geographic region, regardless of harvest intensity* - For four species (Chipping Sparrow, Dark-eyed Junco, Dusky Flycatcher, and Swainson's Thrush) and all species' groups, we had sufficient data to compute specific correlations between abundance and reproduction for at least two regions separately within the Pacific Northwest. Data were pooled across harvest intensities within each region. In this way, therefore, we were able to examine the consistency of relationships between abundance and reproduction across forests of the Pacific Northwest. As when pooling data across regions (Table 16), we found few significant correlations when regions were analyzed separately (Table 17). Further analyses to compare slopes for region-specific relationships also yielded few significant differences (Table 18).

One species that exhibited significant correlations between abundance and nest-level reproduction (Table 17) that differed between regions ($P < 0.05$) of the Pacific Northwest (Table 18) was the Dusky Flycatcher: abundance was significantly positively correlated with nest success (and nest-level productivity) in east-central Washington, but significantly negatively correlated with nest success in west-central Idaho (Table 17, Fig. 21a). In northeast Oregon, abundance and reproduction were uncorrelated.



A. Black-headed Grosbeak

B. House Wren

C. Willow Flycatcher

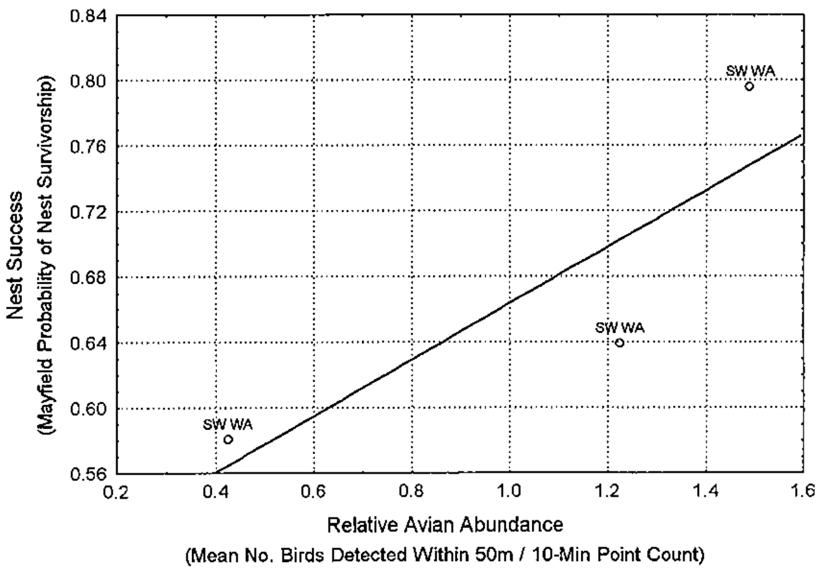
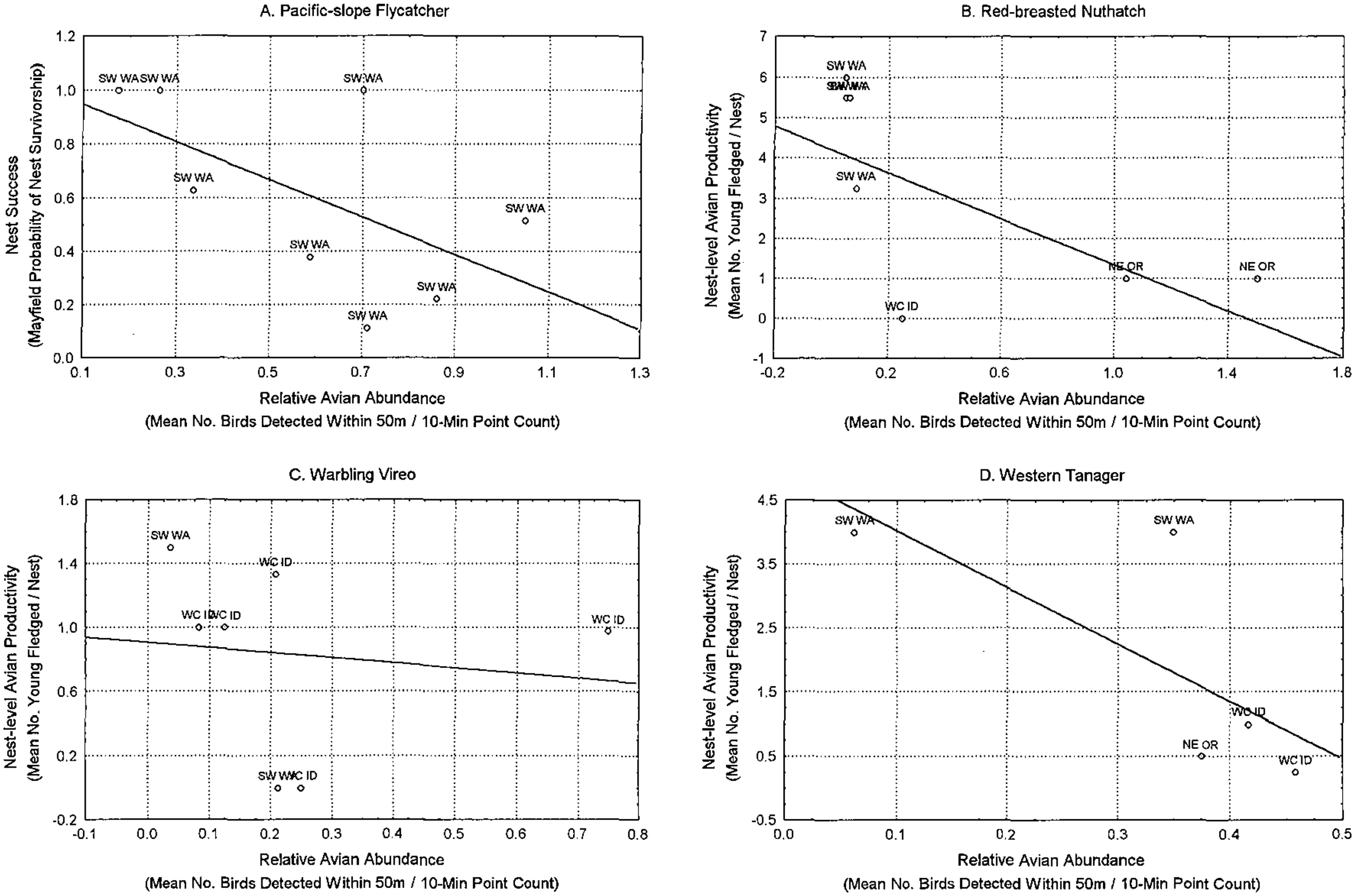


Figure 19. Bird species that exhibited significant positive correlations between relative avian abundance and nest-level reproduction during meta-analysis of data from four regions in the Pacific Northwest. See Table 16 for details of correlation analysis.

Figure 20. Bird species that exhibited significant negative correlations between relative avian abundance and nest-level reproduction during meta-analysis of data from four regions in the Pacific Northwest. See Table 16 for details of correlation analysis.



A. Pacific-slope Flycatcher

B. Red-breasted Nuthatch

C. Warbling Vireo

D. Western Tanager

Table 17. Region-specific spearman rank correlation analysis between relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M) and nest productivity (mean number of young fledged per nest; NESTPROD), and between relative avian abundance and nest success (Mayfield estimates of nest survival; NESTSURV) for four species and 10 species' groups included in Pacific Northwest forests meta-analysis.

Bird Species	PNW	RAB50M vs. NESTPROD			RAB50M vs. NESTSURV		
or Species' Group	Region (*n*)[a]	*r*	*t*	*P*	*r*	*t*	*P*
Dark-eyed Junco	SWWA (9)	0.43	1.27	0.24	0.00	0.00	1.00
	ECWA (6)	0.46	1.05	0.35	-0.03	-0.07	0.95
	NEOR (4)	0.21	0.30	0.79	0.40	0.62	0.60
	WCID (5)	0.36	0.67	0.55	0.36	0.67	0.36
Dusky Flycatcher	ECWA (3)	1.00	---	<0.0001	1.00	---	<0.0001
	NEOR (5)	0.67	1.57	0.22	0.40	0.76	0.50
	WCID (5)	0.10	0.17	0.87	-1.00	---	<0.0001
Chipping Sparrow	NEOR (3)	0.26	0.38	0.74	-0.80	-1.89	0.20
	WCID (5)	0.68	1.63	0.20	0.29	0.52	0.64
Swainson's Thrush	SWWA (5)	-0.62	-1.35	0.27	0.00	0.00	1.00
	WCID (3)	-0.50	0.58	0.67	0.50	0.58	0.67
Resident Birds	SWWA (12)	-0.05	-0.15	0.88	-0.38	-1.32	0.22
	ECWA (6)	-0.81	-2.78	<0.05	-0.68	-1.84	0.14
	NEOR (5)	-0.62	-1.35	0.27	-0.55	-1.15	0.33
	WCID (5)	0.80	2.31	0.10	0.97	7.55	<0.01
Migrant Birds	SWWA (12)	-0.27	-0.90	0.39	-0.15	-0.50	0.63
	ECWA (3)	-0.50	-0.58	0.67	-0.50	-0.58	0.67
	NEOR (6)	-0.33	-0.71	0.52	-0.49	-1.11	0.33
	WCID (5)	0.30	0.54	0.62	-0.20	-0.35	0.75
Open-cup-Nesting Birds	SWWA (12)	-0.32	-1.08	0.31	-0.21	-0.69	0.50
	ECWA (3)	-0.50	-0.58	0.67	-1.00	---	<0.0001
	NEOR (6)	-0.27	-0.57	0.60	-0.43	-0.95	0.40
	WCID (5)	0.21	0.36	0.74	-0.67	-1.55	0.22

Ground-Nesting Birds	SWWA (9)	0.35	0.99	0.36	0.12	0.32	0.76
	ECWA (6)	-0.06	-0.12	0.91	-0.27	-0.56	0.60
	NEOR (4)	0.21	0.30	0.79	0.40	0.62	0.60
	WCID (5)	0.53	1.07	0.36	0.55	1.15	0.33
Cavity-Nesting Birds	SWWA (10)	0.30	0.88	0.40	-0.45	-1.44	0.19
	ECWA(2)	---	---	---	---	---	---
	NEOR (3)	0.00	0.00	1.00	-0.87	-1.73	0.33
	WCID (4)	-0.26	-0.38	0.74	---	---	---
Foliage-Gleaning Birds	SWWA (12)	0.31	1.02	0.33	-0.19	-0.61	0.56
	ECWA (3)	-1.00	---	<0.0001	-1.00	---	<0.0001
	NEOR (6)	-0.42	-0.92	0.41	-0.46	-1.05	0.35
	WCID (5)	0.60	1.30	0.28	0.10	0.17	0.87
Ground-Feeding Birds	SWWA (10)	-0.33	-1.00	0.35	-0.74	-3.13	<0.05
	ECWA (6)	-0.58	-1.41	0.23	-0.51	-1.18	0.30
	NEOR (5)	-0.30	-0.54	0.62	-0.41	-0.78	0.49
	WCID (5)	0.76	2.05	0.13	0.71	1.75	0.18
Bark-Feeding Birds	SWWA (10)	0.52	1.71	0.13	-0.12	-0.35	0.74
	ECWA (1)	---	---	---	---	---	---
	NEOR (2)	---	---	---	---	---	---
	WCID (3)	0.00	0.00	1.00	---	---	---
Aerial-Feeding Birds	SWWA (12)	-0.31	-1.02	0.33	-0.27	-0.90	0.39
	ECWA (3)	1.00	---	<0.0001	1.00	---	<0.0001
	NEOR (5)	0.67	1.57	0.22	0.40	0.76	0.50
	WCID (5)	0.10	0.17	0.87	-1.00	---	<0.0001
All Species Combined	SWWA (12)	-0.21	-0.68	0.51	-0.46	-1.65	0.13
	ECWA (6)	-0.81	-2.78	<0.05	-0.52	-1.22	0.29
	NEOR (6)	-0.77	-2.42	<0.10	-0.31	-0.66	0.54
	WCID (5)	0.36	0.67	0.55	-0.10	-0.18	0.87

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[a] Number in parenthesis is the number of study plots in each region, which are defined as follows: southwestern Washington (SWWA); east-central Washington (ECWA); northeast Oregon (NEOR); and west-central Idaho (WCID).

Table 18. Region-specific slope and intercept comparisons for relationships between relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M) and nest productivity (mean number of young fledged per nest; NESTPROD), and between relative avian abundance and nest success (Mayfield estimates of nest survival; NESTSURV) for four species and 10 species' groups included in Pacific Northwest forests meta-analysis. For each comparison, slopes (*b*) and intercepts (*a*) are tested for statistical differences among regions. Samples sizes (*n*) are given only on the first line of data for each species or species' group.

Bird Species or Species' Group	Variable Comparison		Value of slope (*b*) and intercept (*a*), by PNW region[a]				Test Statistic[b]	*P*[c]
			SWWA	ECWA	NEOR	WCID		
Dark-eyed Junco	RAB50M *vs.*	*b*	.9663 (9)	.7099 (6)	-.6276 (4)	1.8571 (5)	$F_{(3,16)} = .3755$	>.5
	NESTPROD	*a*	1.7592	1.4685	2.0414	1.3381	$F_{(3,19)} = 1.2775$	>.5
	RAB50M *vs.*	*b*	-.1924	-.1414	-.3911	.2864	$F_{(3,16)} = .2302$	>.5
	NESTSURV	*a*	.6095	.7906	.7133	.5037	$F_{(3,19)} = .7976$	>.5
Dusky Flycatcher	RAB50M *vs.*	*b*		.9679 (3)	.3827 (5)	-.0976 (5)	$F_{(2,7)} = .1272$	>.5
	NESTPROD	*a*		.1466	.2618	1.0421	$F_{(2,9)} = .3953$	>.5
	RAB50M *vs.*	*b*		.5771	.0935	-1.2141	$F_{(2,7)} = 7.4860$	$.02 < P < .05$
	NESTSURV	*a*		.0305	.1813	1.2978	$F_{(2,9)} = .8253$	>.5
Chipping Sparrow	RAB50M *vs.*	*b*			0.0000 (4)	3.5319 (5)	$t_{(5)} = 1.4838$	$.1 < P < .2$
	NESTPROD	*a*			.0625	.4833	$t_{(6)} = 2.7745$	$.02 < P < .05$
	RAB50M *vs.*	*b*			-.2337	.6394	$t_{(5)} = .8466$	$.2 < P < .5$
	NESTSURV	*a*			.3803	.4165	$t_{(6)} = 1.9950$	$.05 < P < .10$
Swainson's Thrush	RAB50M *vs.*	*b*	-4.2529 (5)			-3.1154 (3)	$t_{(4)} = .1748$	>.5
	NESTPROD	*a*	3.6825			1.8750	$t_{(5)} = .1598$	>.5
	RAB50M *vs.*	*b*	.1187			.0969	$t_{(4)} = .0144$	>.5
	NESTSURV	*a*	.9065			.3782	$t_{(5)} = 2.4016$	$.05 < P < .10$

Resident Birds	RAB50M *vs.*	*b*	-.7055 (12)	-1.5538 (6)	-2.6892 (5)	2.3576 (5)	$F_{(3,20)} = .7243$	>.5
	NESTPROD	*a*	2.9709	2.1541	3.7254	.7410	$F_{(3,23)} = 3.1141$	$.05 < P < .10$
	RAB50M *vs.*	*b*	-.3978	-1.4189	-1.0090	-.9393	$F_{(3,20)} = 3.2813$	$.05 < P < .10$
	NESTSURV	*a*	.8291	1.2978	1.4941	.4425	$F_{(3,23)} = .3556$	>.5
Migrant Birds	RAB50M *vs.*	*b*	-1.7547 (12)	-2.4757 (3)	-.6628 (6)	1.1592 (5)	$F_{(3,18)} = .3983$	>.5
	NESTPROD	*a*	2.9541	1.9563	.8792	.4075	$F_{(3,21)} = 6.5122$	$<.005 < P < .01$
	RAB50M *vs.*	*b*	-.2850	.0342	-.4013	-.7171	$F_{(3,18)} = .1440$	>.5
	NESTSURV	*a*	.8084	.4490	.5237	.8192	$F_{(3,21)} = 2.6120$	$.1 < P < .2$
Open-cup-Nesting Birds	RAB50M *vs.*	*b*	-1.0125 (12)	-1.7074 (3)	-.5629 (6)	1.2312 (5)	$F_{(3,18)} = .3224$	>.5
	NESTPROD	*a*	2.2845	1.7857	.9267	.3833	$F_{(3,21)} = 5.0229$	$.01 < P < .02$
	RAB50M *vs.*	*b*	-.3394	-.2197	-.3328	-1.2457	$F_{(3,18)} = .2463$	>.5
	NESTSURV	*a*	1.3043	.5798	.5154	.9947	$F_{(3,21)} = 1.2556$	>.5
Ground-Nesting Birds	RAB50M *vs.*	*b*	.9202 (9)	.4445 (6)	-.6276 (4)	3.0119 (5)	$F_{(3,16)} =1.0427$	>.5
	NESTPROD	*a*	1.7507	1.5321	2.0414	.6537	$F_{(3,19)} = 1.0803$	>.5
	RAB50M *vs.*	*b*	.1988	-.3973	-.3911	.6212	$F_{(3,16)} = .7130$	>.5
	NESTSURV	*a*	.5930	.9139	.7133	.3224	$F_{(3,19)} = .7639$	>.5
Cavity-Nesting Birds	RAB50M *vs.*	*b*	1.6590 (10)		-.1319 (3)	-.8827 (4)	$F_{(2,11)} = .3352$	>.5
	NESTPROD	*a*	2.6485		1.1181	.5359	$F_{(2,13)} = 20.5641$	<.001
	RAB50M *vs.*	*b*	-.2405		-1.2439	0.0000	$F_{(2,11)} = 3.6736$	$.10 < P < .20$
	NESTSURV	*a*	.9098		1.6090	1.0000	$F_{(2,13)} = .5178$	>.5
Foliage-Gleaning Birds	RAB50M *vs.*	*b*	1.2791 (12)	-.81127 (3)	-.7857 (6)	.8108 (5)	$F_{(3,18)} = 5.0854$	$.01< P < .05$
	NESTPROD	*a*	1.6085	4.0012	1.0234	.5467	$F_{(3,21)} = 80509$	$.001 < P < .002$
	RAB50M *vs.*	*b*	-.0929	-.8028	-.4663	-.1522	$F_{(3,18)} = .5285$	>.5
	NESTSURV	*a*	.6441	1.0006	.6844	.5933	$F_{(3,21)} = 1.9361$	$.2 < P < .5$

Ground-Feeding Birds	RAB50M *vs.*	*b*	-1.5299 (10)	-1.3623 (6)	-.6524 (5)	-.3802 (5)	$F_{(3,18)} = 3.1587$	$.1 < P < .2$
	NESTPROD	*a*	2.4531	2.2194	2.1505	.6362	$F_{(3,21)} = .2145$	>.50
	RAB50M *vs.*	*b*	-.9908	-1.1237	-.6133	.6586	$F_{(3,18)} = 3.1023$	$.1 < P < .2$
	NESTSURV	*a*	.6959	1.2201	.9509	.2949	$F_{(3,21)} = .2404$	>.5
Bark-Feeding Birds	RAB50M *vs.*	*b*	7.5831 (10)			.6606 (3)	$t_{(9)} = .9782$	>.5
	NESTPROD	*a*	2.7595			.4128	$t_{(10)} = 4.6546$	<.001
	RAB50M *vs.*	*b*	.0740			0.0000	$t_{(9)} = .0679$	>.5
	NESTSURV	*a*	.8849			1.0000	$t_{(10)} = .9985$	$.2 < P < .5$
Aerial-Feeding Birds	RAB50M *vs.*	*b*	-.4199 (12)	.9679 (3)	.3827 (5)	-.0976 (5)	$F_{(3,17)} = .2858$	>.5
	NESTPROD	*a*	2.0426	.1466	.2618	1.0421	$F_{(3,20)} = 3.5724$	$< .05 < P < .10$
	RAB50M *vs.*	*b*	-.0736	.5771	.0935	-1.2141	$F_{(3,17)} = 2.9333$	$.1 < P < .2$
	NESTSURV	*a*	1.1316	.0305	.1813	1.2798	$F_{(3,20)} = 2.9600$	$.1 < P < .2$
All Species Combined	RAB50M *vs.*	*b*	-1.9932 (12)	-3.3898 (6)	-1.1630 (6)	.8329 (5)	$F_{(3,21)} = .5206$	>.5
	NESTPROD	*a*	3.4327	2.6908	1.5706	.6935	$F_{(3,24)} = 15.1965$	<.001
	RAB50M *vs.*	*b*	-.3396	-1.6013	-.5311	-.1646	$F_{(3,21)} = 1.0650$	>.5
	NESTSURV	*a*	.6544	1.2363	.7622	.5211	$F_{(3,24)} = 1.1942$	>.5

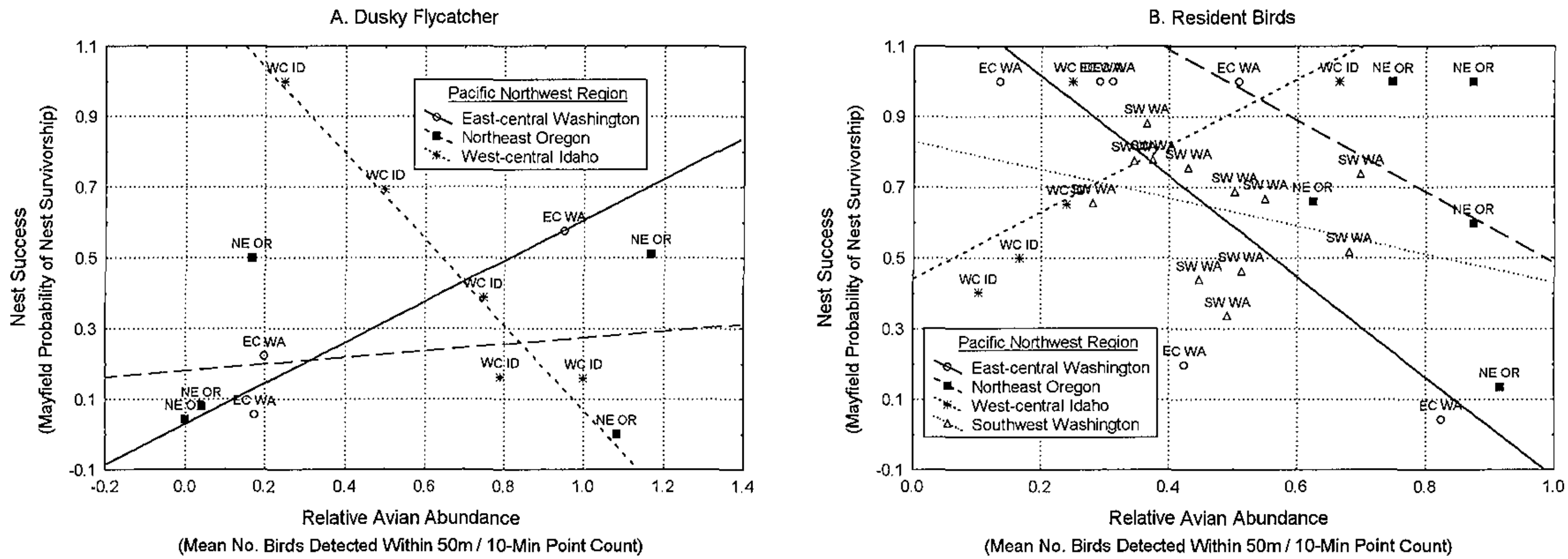
[a] Southwestern Washington (SWWA); east-central Washington (ECWA); northeast Oregon (NEOR); and west-central Idaho (WCID).

[b] For comparisons between two regions, we used a Student's *t*-test to compare slopes and intercepts; when there were sufficient data to allow comparisons among more than two regions, we used an *F*-test (Zar 1996). Because regression statistics (e.g., regression coefficients, *b*) and *t*- and *F*-tests are known to be robust with respect to deviations from normality and homoscedasticity (e.g., Jacques and Norusis 1973), we chose to use parametric tests throughout these analyses.

[c] *P*-values are given as ranges rather than exact numbers because these tests were performed by hand and critical values of test statistics were compared with observed values using standard statistical tables (Rohlf and Sokal 1981).

A. Dusky Flycatcher

B. Resident Birds



C. Foliage-Gleaning Birds

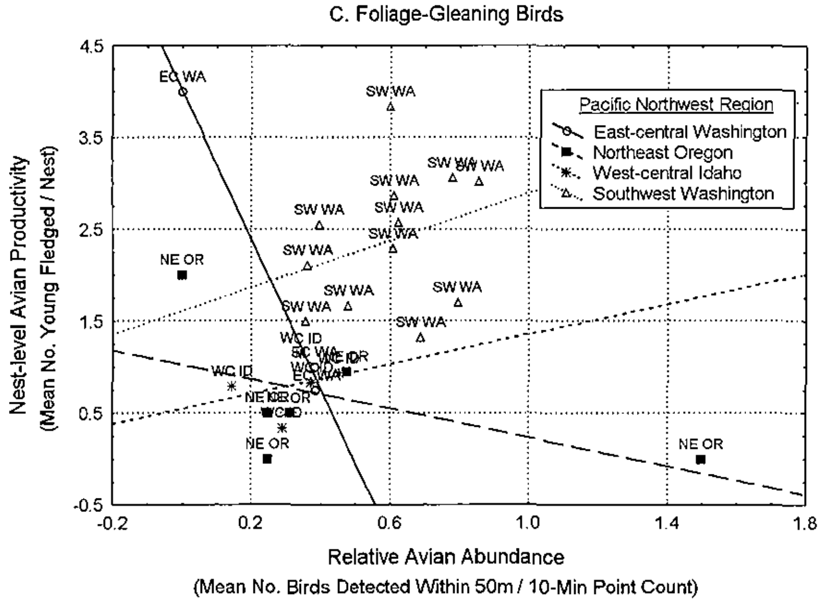


Figure 21. Bird species or species' groups that exhibited significantly different relationships (as judged by statistical comparisons of slopes) between relative avian abundance and nest-level reproduction in different regions of the Pacific Northwest. See Table 17 for correlation analysis and Table 18 for slope comparisons.

Likewise, the relative abundance of resident birds as a whole was significantly positively correlated with nest success in west-central Idaho, but uncorrelated in other regions of the Pacific Northwest (Table 17, Fig. 21b); these relationships were statistically different ($P < 0.10$) among regions according to slope comparisons (Table 18). Finally, foliage-gleaning birds exhibited significant negative correlations between abundance and nest-level productivity in east-central Washington, but no significant correlations between these two population measures elsewhere in the Pacific Northwest (Table 17, Fig. 21c). These region-specific differences also were statistically significant ($P < 0.05$; Table 18). These results suggest that while most bird species and/or species' groups may exhibit similar relationships between abundance and reproduction across the Pacific Northwest, there are some for which such relationships may be region-dependent. The implication of these findings for our study is that survey techniques may work well in some regions for some species, but not in others.

4.4.3. *Effects of harvest intensity, regardless of geographic region* - For seven species (American Robin, Brown Creeper, Chestnut-backed Chickadee, Dark-eyed Junco, Hairy Woodpecker, Pacific-slope Flycatcher, and Winter Wren) and all species' groups, we also examined relationships between abundance and reproduction for at least two harvest intensities separately within the Pacific Northwest. Data were pooled across regions within each harvest intensity. Again, we found few significant correlations between abundance and reproduction (Table 19) and few significantly different slopes for harvest-intensity-specific relationships (Table 20). We had insufficient data to compute correlations between abundance and reproduction for region x harvest intensity comparisons.

The Winter Wren was the only bird species for which the relationship between abundance and nest-level reproduction differed significantly between harvest intensities (Table 20). This result is consistent with our earlier finding for this species that the relationship between abundance and area-level productivity differed significantly between forest treatments (Fig. 14e). When analyzing nest-level data, although our analyses were still limited to data from the southwest Cascade Mountains of Washington because of the wren's distribution, abundance and reproduction were significantly positively correlated at no harvest intensity (e.g., old growth), but uncorrelated at moderate harvest intensity (e.g., commercial thins; Table 19, Fig. 22a). Similar results were found for the relationship between wren abundance and nest success (Table 19, Fig. 22b). For this interesting species, therefore, regardless of how we choose to measure reproduction, the reliability of point-count surveys to accurately reflect habitat quality appears questionable. If one wanted to compare the effects of timber harvest on winter wren population health and viability, using point counts to do so could be especially misleading.

Table 19. Harvest-intensity-specific spearman rank correlation analysis between relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M) and nest productivity (mean number of young fledged per nest; NESTPROD), and between relative avian abundance and nest success (Mayfield estimates of nest survival; NESTSURV) for seven species and 10 species' groups included in Pacific Northwest forests meta-analysis.

Bird Species	Harvest	RAB50M v NESTPROD			RAB50M v NESTSURV		
or Species' Group	Intensity (*n*)[a]	*r*	*t*	*P*	*r*	*t*	*P*
Dark-eyed Junco	None (6)	-0.18	-0.36	0.74	-0.85	-3.16	<0.05
	Moderate (15)	0.22	0.83	0.42	0.33	1.25	0.23
	High (3)	1.00	---	<0.0001	1.00	---	<0.0001
American Robin	Moderate (8)	0.11	0.27	0.80	-0.12	-0.30	0.77
	High (4)	0.74	1.55	0.26	0.60	1.06	0.40
Brown Creeper	None (4)	-0.33	-0.50	0.67	0.82	2.00	0.18
	Moderate (4)	0.20	0.29	0.80	-0.32	-0.47	0.68
Chestnut-backed Chick.	None (3)	-0.87	-1.73	0.33	-0.87	-1.73	0.33
	Moderate (3)	1.00	---	<0.0001	---	---	---
Hairy Woodpecker	None (3)	0.00	0.00	1.00	---	---	---
	Moderate (5)	0.56	1.18	0.32	-0.35	-0.65	0.56
Pacific-slope Flycatcher	None (4)	-0.80	-1.89	0.20	-0.74	-1.55	0.26
	Moderate (4)	-0.2	-0.29	0.80	-0.80	-1.89	0.20
Winter Wren	None (4)	1.00	---	<0.0001	1.00	---	<0.0001
	Moderate (4)	0.20	0.29	0.80	-0.40	-0.62	0.60
Resident Birds	None (8)	0.13	0.33	0.76	-0.85	-3.96	<0.01
	Moderate (16)	0.16	0.59	0.56	0.07	0.26	0.80
	High (4)	-0.40	-0.62	0.60	-0.40	-0.62	0.60
Migrant Birds	None (5)	0.30	0.54	0.62	0.41	0.78	0.49
	Moderate (16)	-0.26	-1.02	0.33	-0.31	-1.21	0.25
	High (5)	-0.80	-2.31	0.10	-0.90	-3.58	<0.05

Open-cup-Nesting Birds	None (5)	0.00	0.00	1.00	0.00	0.00	1.00
	Moderate (16)	-0.21	-0.79	0.44	-0.32	-1.26	0.23
	High (5)	-0.70	-1.70	0.19	-1.00	---	<0.0001
Ground-Nesting Birds	None (6)	-0.18	-0.36	0.74	-0.85	-3.16	<0.05
	Moderate (15)	0.34	1.31	0.21	0.32	1.20	0.25
	High (3)	1.00	---	<0.0001	1.00	---	<0.0001
Cavity-Nesting Birds	None (5)	0.60	1.30	0.28	-0.10	-0.17	0.87
	Moderate (12)	0.40	1.36	0.20	-0.75	-3.57	<0.01
	High (2)	---	---	---	---	---	---
Foliage-Gleaning Birds	None (5)	0.90	3.58	<0.05	-0.60	-1.30	0.28
	Moderate (16)	0.25	0.97	0.35	0.20	0.77	0.45
	High (5)	-0.70	-1.70	0.19	-0.80	-2.31	0.10
Ground-Feeding Birds	None (6)	-0.44	-0.98	0.38	-0.85	-3.16	<0.05
	Moderate (16)	0.12	0.45	0.66	-0.06	-0.21	0.84
	High (4)	-0.80	-1.89	0.20	-0.80	-1.89	0.20
Bark-Feeding Birds	None (4)	0.40	0.62	0.60	0.77	1.73	0.23
	Moderate (10)	-0.02	-0.04	0.97	0.01	0.04	0.97
	High (2)	---	---	---	---	---	---
Aerial-Feeding Birds	None (5)	0.00	0.00	1.00	0.05	0.09	0.93
	Moderate (15)	0.23	0.86	0.40	0.08	0.30	0.77
	High (5)	0.10	0.17	0.87	-0.50	-1.00	0.39
All Species Combined	None (8)	-0.13	-0.33	0.76	-0.87	-4.41	<0.01
	Moderate (16)	0.04	0.16	0.88	0.26	1.03	0.32
	High (5)	-0.70	-1.70	0.19	-0.90	-3.58	<0.05

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[a] Number in parenthesis is the number of study plots in each harvest intensity, which are defined as follows: mature and old-growth forests (none); commercially-thinned forests (moderate); and clearcuts (high).

Table 20. Harvest-intensity-specific slope and intercept comparisons for relationships between relative avian abundance (number of birds detected within 50m / 10-min point count; RAB50M) and nest productivity (mean number of young fledged per nest; NESTPROD), and between relative avian abundance and nest success (Mayfield estimates of nest survival; NESTSURV) for seven species and 10 species' groups included in Pacific Northwest forests meta-analysis. For each comparison, slopes (*b*) and intercepts (*a*) are tested for statistical differences among harvest intensities. Samples sizes (*n*) are given only on the first line of data for each species or species' group.

Bird Species or Species' Group	Variable Comparison		Harvest Intensity[a] None	Moderate	High	Test Statistic[b]	P[c]
Dark-eyed Junco	RAB50M *vs.*	*b*	-.7962(6)	.9588 (15)	2.3701(3)	$F_{(2,18)} = 1.1282$	>.5
	NESTPROD	*a*	2.1080	1.4381	.6840	$F_{(2,20)} = .2540$	>.5
	RAB50M *vs.*	*b*	-.7173	.3202	.7467	$F_{(2,18)} = 1.4030$	>.5
	NESTSURV	*a*	1.0171	.3617	.2645	$F_{(2,20)} = 2.1368$	$.2 < P < .5$
American Robin	RAB50M *vs.*	*b*		.8397 (8)	7.8420 (4)	$t_{(10)} = 1.1633$	$.2 < P < .5$
	NESTPROD	*a*		1.3371	-.9356	$t_{(9)} = .8180$	>.5
	RAB50M *vs.*	*b*		-.2088	2.5321	$t_{(10)} = .5819$	>.5
	NESTSURV	*a*		.5608	-.2941	$t_{(9)} = .5642$	>.5
Brown Creeper	RAB50M *vs.*	*b*	-13.0707 (4)	-1.2649 (4)		$t_{(5)} = 1.0078$	$.2 < P < .5$
	NESTPROD	*a*	9.8947	3.8435		$t_{(5)} = 1.4555$	$.2 < P < .5$
	RAB50M *vs.*	*b*	.3455	-1.7433		$t_{(5)} = .6825$	>.5
	NESTSURV	*a*	.8320	.9627		$t_{(5)} = 2.0839$	$.05 < P < .10$
Chestnut-back. Chickadee	RAB50M *vs.*	*b*	-29.9822 (3)	5.9563 (3)		$t_{(2)} = 4.6208$	$.10 < P < .20$
	NESTPROD	*a*	26.6148	-.3415		$t_{(3)} = 3.1820$	$P = .05$
	RAB50M *vs.*	*b*	-3.9058	0.0000		$t_{(2)} = 3.9120$	$.05 < P < .10$
	NESTSURV	*a*	3.6204	1.0000		$t_{(3)} = .6066$	>.5
Hairy Woodpecker	RAB50M *vs.*	*b*	.8384 (3)	10.6887 (5)		$t_{(4)} = .0520$	>.5
	NESTPROD	*a*	2.9769	.4518		$t_{(5)} = 2.5776$	$.02 < P < .05$
	RAB50M *vs.*	*b*	0.0000	-.8782		$t_{(4)} = .1350$	>.5
	NESTSURV	*a*	1.0000	.9286		$t_{(5)} = 1.8847$	$.1 < P < .2$

Pacific-slope Flycatcher	RAB50M *vs.*	*b*	-.43119 (4)	-.9151 (4)		$t_{(4)} = 1.0540$	$.2 < P < .5$
	NESTPROD	*a*	4.9100	2.4411		$t_{(5)} = .5052$	>.5
	RAB50M *vs.*	*b*	-1.0445	-.4565		$t_{(4)} = .6361$	>.5
	NESTSURV	*a*	1.2226	.8860		$t_{(5)} = .0189$	>.5
Winter Wren	RAB50M *vs.*	*b*	3.4638 (4)	.1182 (4)		$t_{(4)} = 3.4548$	$.02 < P < .05$
	NESTPROD	*a*	-2.5492	2.0478		$t_{(5)} = .4207$	>.5
	RAB50M *vs.*	*b*	.7807	-.1117		$t_{(4)} = 2.7348$	$.05 < P < .10$
	NESTSURV	*a*	-.6206	.5551		$t_{(5)} = .4377$	>.5
Resident Birds	RAB50M *vs.*	*b*	-.5385 (8)	.2438 (16)	-1.2918 (4)	$F_{(2,22)} = .1102$	>.5
	NESTPROD	*a*	2.8281	1.6416	2.2800	$F_{(2,24)} = 1.7847$	$.2 < P < .5$
	RAB50M *vs.*	*b*	-.4869	-.1393	-.5770	$F_{(2,22)} = .2292$	> .5
	NESTSURV	*a*	.9621	.7494	-.5770	$F_{(2,24)} = .7795$	> .5
Migrant Birds	RAB50M *vs.*	*b*	1.7134 (5)	-1.5139 (16)	-2.265 (5)	$F_{(2,20)} = .3849$	>.5
	NESTPROD	*a*	1.3660	1.8232	3.1960	$F_{(2,22)} = .8835$	>.5
	RAB50M *vs.*	*b*	1.0091	-.4115	-.9332	$F_{(2,20)} = 1.7807$	$.2 < P < .5$
	NESTSURV	*a*	.2988	.6873	1.2462	$F_{(2,22)} = .8244$	>.5
Open-cup-Nesting Birds	RAB50M *vs.*	*b*	3.2986 (5)	-1.2020 (16)	-1.6373 (5)	$F_{(2,20)} = .5783$	>.5
	NESTPROD	*a*	.7614	1.6589	2.4327	$F_{(2,22)} = .5023$	>.5
	RAB50M *vs.*	*b*	.7458	-.5245	-.6600	$F_{(2,20)} = .9548$	>.5
	NESTSURV	*a*	.3516	.6387	.9122	$F_{(2,22)} = .1870$	>.5
Ground-Nesting Birds	RAB50M *vs.*	*b*	-.7962 (6)	1.3977 (15)	3.1056 (3)	$F_{(2,18)} = 1.5866$	$.2 < P < .5$
	NESTPROD	*a*	2.1080	1.0801	.0253	$F_{(2,20)} = .0995$	>.5
	RAB50M *vs.*	*b*	-.7173	.3234	1.4015	$F_{(2,18)} = 3.0112$	$.1 < P < .2$
	NESTSURV	*a*	1.0171	.3598	-.2658	$F_{(2,20)} = .6746$	>.5
Cavity-Nesting Birds	RAB50M *vs.*	*b*	2.4920 (5)	2.3503 (12)		$t_{(13)} = .0442$	>.5
	NESTPROD	*a*	2.1420	.7111		$t_{(14)} = 1.9511$	$.05 < P < .10$
	RAB50M *vs.*	*b*	-.0582	-.5151		$t_{(13)} = 1.7882$	$.05 < P < .10$
	NESTSURV	*a*	.8761	1.0760		$t_{(14)} = 1.3296$	$.2 < P < .5$

Foliage-Gleaning Birds	RAB50M *vs.*	*b*	5.7812 (5)	.9550 (16)	-1.7390 (5)	$F_{(2,20)} = 3.0386$	$.10 < P < .50$
	NESTPROD	*a*	-1.1407	1.1760	2.6886	$F_{(2,22)} = .9595$	>.5
	RAB50M *vs.*	*b*	-.1218	-.0590	-.5834	$F_{(2,20)} = 1.2399$	>.5
	NESTSURV	*a*	.6147	.6534	.8727	$F_{(2,22)} = .1586$	>.5
Ground-Feeding Birds	RAB50M *vs.*	*b*	-.8793 (6)	1.0241 (16)	-3.1327 (4)	$F_{(2,20)} = 1.2272$	>.5
	NESTPROD	*a*	2.1808	1.2873	3.0583	$F_{(2,22)} = .0392$	>.5
	RAB50M *vs.*	*b*	-.7158	.0746	-1.118	$F_{(2,20)} = 1.4842$	>.5
	NESTSURV	*a*	1.0150	.5211	1.0520	$F_{(2,22)} = .3988$	>.5
Bark-Feeding Birds	RAB50M *vs.*	*b*	4.5816 (4)	-.6892 (10)		$t_{(10)} = .5351$	>.5
	NESTPROD	*a*	3.7771	2.0747		$t_{(11)} = 3.2077$	$.005 < P < .01$
	RAB50M *vs.*	*b*	.1455	.0831		$t_{(10)} = .0634$	>.5
	NESTSURV	*a*	.9562	.8759		$t_{(11)} = 1.0665$	$.2 < P < .5$
Aerial-Feeding Birds	RAB50M *vs.*	*b*	-1.2550 (5)	.4223 (15)	-.0779 (5)	$F_{(2,19)} = .3081$	>.5
	NESTPROD	*a*	2.1074	.7580	1.6107	$F_{(2,21)} = 1.1128$	>.5
	RAB50M *vs.*	*b*	-.3449	.0048	-.3441	$F_{(2,19)} = .3229$	>.5
	NESTSURV	*a*	.6371	.4202	.9791	$F_{(2,21)} = 1.2944$	>.5
All Species Combined	RAB50M *vs.*	*b*	-.2185 (8)	.0028 (16)	-2.2441 (5)	$F_{(2,23)} = .5501$	>.5
	NESTPROD	*a*	2.3771	1.5047	2.9978	$F_{(2,25)} = 1.9862$	>.5
	RAB50M *vs.*	*b*	-1.3596	.2747	-.7858	$F_{(2,23)} = 4.1251$	$.05 < P < .10$
	NESTSURV	*a*	1.2074	.4909	1.0434	$F_{(2,25)} = .5553$	>.5

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[a] Harvest intensities defined as follows: mature and old-growth forests (none); commercially-thinned forests (moderate); and clearcuts (high).

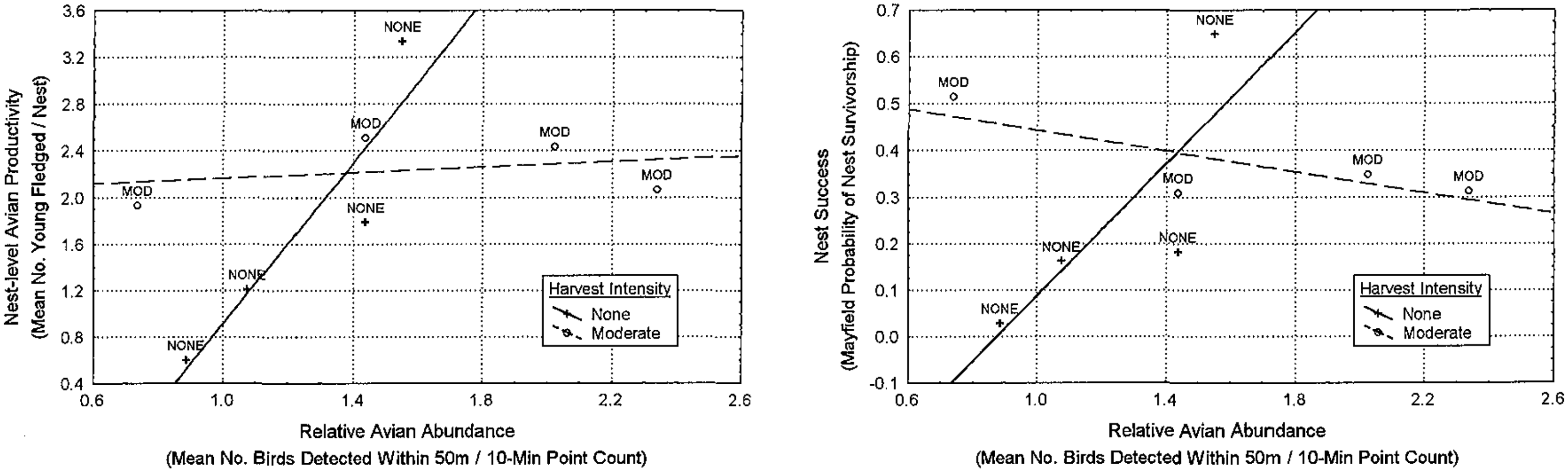
[b] For comparisons between two harvest intensities, we used a Student's *t*-test to compare slopes and intercepts; when there were sufficient data to allow comparisons among all three harvest intensities, we used an *F*-test (Zar 1996). Because regression statistics (e.g., regression coefficients, *b*) and *t*- and *F*-tests are known to be robust with respect to deviations from normality and homoscedasticity (e.g., Jacques and Norusis 1973), we chose to use parametric tests throughout these analyses.

[c] *P*-values are given as ranges rather than exact numbers because these tests were performed by hand and critical values of test statistics were compared with observed values using standard statistical tables (Rohlf and Sokal 1981).

Figure 22. Bird species or species' groups that exhibited significantly different relationships (as judged by statistical comparisons of slopes) between relative avian abundance and nest-level reproduction in different forest treatments of the Pacific Northwest. See Table 19 for correlation analysis and Table 20 for slope comparisons.

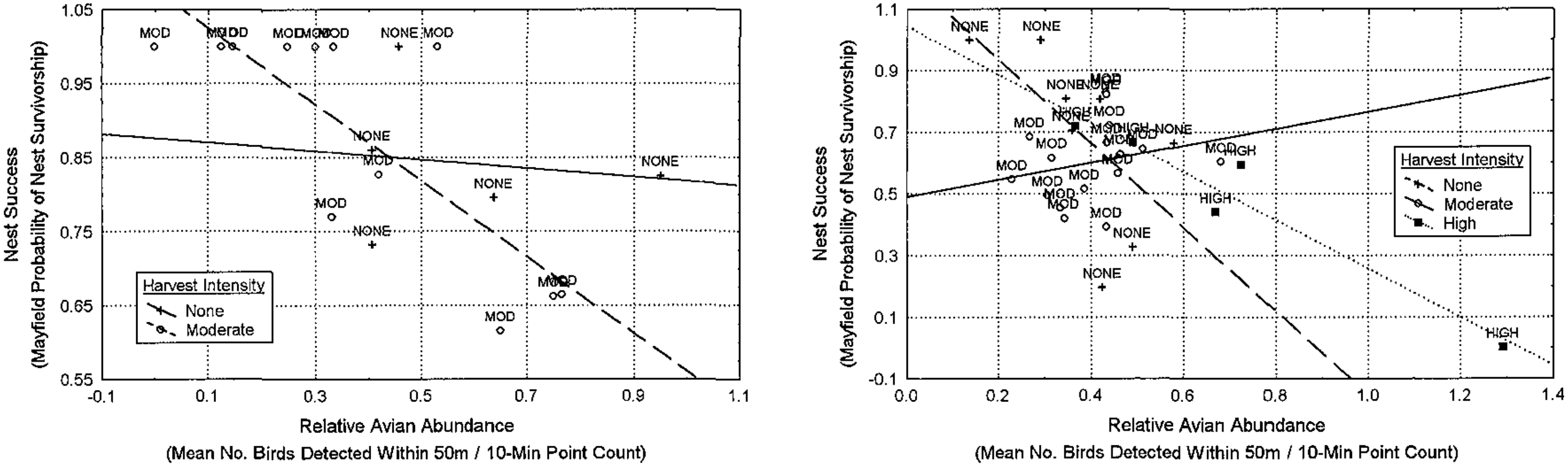
A. Winter Wren - Productivity

B. Winter Wren - Nest Success



C. Cavity-Nesting Birds

D. All Bird Species Combined



Like the Winter Wren, cavity-nesting birds had significantly different ($P < 0.10$) relationships between abundance and nest success for none and moderate harvest intensities (Table 20, Fig. 22c). These relationships were uncorrelated at no harvest intensities, but significantly negatively correlated at moderate harvest intensities (Table 19). And finally, significant differences ($P < 0.10$) were found between all three harvest intensities for relationships between abundance and nest success of all breeding birds combined (Table 20). Abundance and nest success were similarly significantly negatively correlated between none and high harvest intensities, but uncorrelated in moderate harvest intensities (Table 19, Fig. 22d).

Overall, these significant patterns should caution researchers that a point count in a thinned forest may not provide the same information as a point count in a stand of old growth. Indeed, our results suggest that, for all species combined, if one were using point counts to assess community health, data collected from extremes of the harvest intensity spectrum (i.e., none and high) might be highly misleading. That is, where one found more birds in general, the quality of habitat (as measured by nest success) would be lower because of the density-dependent relationship between abundance and Mayfield nest success (Fig. 22d). When interpreting the results of our meta-analysis as we describe them here, we again remind readers that we could not use what we consider to be the best measure of habitat quality (i.e., area-level productivity) because we did not have the data to compute it (see above).

4.4.4. *Expanded meta-analysis* - Our general lack of significant results when combining data for forest birds across the Pacific Northwest implies one of two things (or perhaps a mix of both): (1) for the most part (i.e., for most species, regardless of region and/or forest condition), point-count surveys are an adequate tool with which to measure habitat quality (because nest-level reproductive success was density independent; area-level productivity would therefore be higher where there were more birds, and presumably, more nests); or (2) we had insufficient data to detect statistically significant relationships due to a lack of power. When one fails to reject a null hypothesis, it has become increasingly common to inquire about the power of a statistical test by performing a retrospective power analysis. Such an analysis is thought to help distinguish between failing to reject a null hypothesis that was actually true (i.e., no real effect existed), and incorrectly failing to reject a null hypothesis that was actually false (i.e., a Type II error). Unfortunately, estimating power from the same data used to test the original null hypothesis is meaningless because both the estimate of power and the *P*-value of the statistical test are determined by sample size and the observed effect size (Steidl et al. 1997). For this reason, power has often been estimated incorrectly for null hypotheses not rejected (Hayes and Steidl 1997) and retrospective power analysis is not an appropriate remedy for the lack of statistical significance that we report here. To better address the issue of low power, we intend to more than double sample sizes in the meta-analysis conducted here by adding data from elsewhere in Idaho and Montana when it is available for analysis and publication. This data set, which was originally collected to address the effects of forest fragmentation on avian productivity in the inland Pacific Northwest (Sallabanks et al. 1999), includes information on 2,847 nests of 66 bird species and will add 32 study plots (12 in west-central Idaho, 12 in northern Idaho, and 8 in western Montana) to the current meta-analysis data set containing 31 study plots (Table 13).

5. Vocalization Rate - Song Output Study

Point-count surveys are used frequently for monitoring forest passerine birds in the Pacific Northwest (Huff and Raley 1991, Manuwal and Carey 1991, Aubry et al. 1997, O'Connell et al. 2000, Pearson and Manuwal 2001) and elsewhere (Verner 1985, Sallabanks et al. 2000b). Point counts in the forest of the Pacific Northwest, which rely mostly on song counts as opposed to visual detections, are mostly used to compare habitat value for particular species. Higher relative abundance of a species based on song counts is commonly interpreted as meaning better habitat quality for that species. Song counts also have been used to make conclusions about habitat preference (Freemark and Collins 1992), population changes (Johnston and Hagan 1992), and fragmentation effects (Blake and Karr 1987).

There are two important assumptions of using relative abundance, as measured by song counts, to compare quality of different habitat types. The first is that individuals of a bird species are equally detectable among different forest habitat types, (i.e., vocalizations are attenuated in similar ways such that individuals birds can be heard at similar distances, and birds behave in similar ways with respect to the observer; Caughley 1977). The second assumption, implicit and often unstated, is that song rates as a measure of young fledged per individual detected are equal among stands. Using song count data to estimate the density of a species based on that species- and habitat type-specific detection function, will help address the first assumption (see Buckland et al. 1993). However, the second assumption is more difficult to address because male song rates, and thus potentially their detection probability, can vary for a variety of reasons. Male song rate in several species has been correlated with the nesting stage (Field Sparrow [*Spizella pusilla*], Best 1981; House Wren, Wilson and Bart 1985; Wood Warbler [*Phyllocopus sibilatrix*], Termin 1986; Barn Swallow [*Hirundo rustica*], Møller 1991). Unpaired males seeking mates sing more often than paired males for a number of species (White-winged Dove [*Zenaida asiatica*], Rappole and Waggerman 1986; Kentucky Warbler [*Oporornis formosus*]; Ovenbird [*Seiurus aurocapillus*], Gibbs and Wenny 1993). The physiological state of birds can also affect its song rate. Food-supplemented male Pied

Flycatchers (*Ficedula hypoleuca*) sang more than control males (Gottlander 1987), and call rates have been correlated with parasite load in Barn Swallows (Møller 1991). Finally, song rate may be related to population density and habitat patch size (McShea and Rappole 1997). Thus while it is conceivable that higher song rates could mean better habitat (e.g., more food = higher fledging rate), high song rates can also be associated with relatively poorer habitat (Best 1981). Unfortunately, the factors affecting song rate and presumably the probability of detection are beyond the scope of typical point count surveys.

The purpose of this preliminary study was to examine factors affecting song rates in the Winter Wren and Song Sparrow. Specifically, we explored the relationship between breeding and mating status on song rates in both species, and the relationship between forest type *per se* (old-growth forest versus commercially thinned 40–60 year-old forest) on Winter Wren song rates.

5.1. Recording Bird Behavior

5.1.1. ***Field protocols (vocalization rate/ song output)*** - We conducted focal observations on Winter Wrens in four forest stands: two stands of old-growth forest and two stands of 40–60 year-old forest that had been commercially thinned (hereafter thinned), and on Song Sparrows in two recently clearcut stands. Focal observations were conducted by recording all vocalizations by a target species within 50 m of an observer for 30 min (hereafter focal session). The observer was positioned at a predetermined location in the stands, either centered within existing bird territories or near the edge of two or more presumed territories, but at least 100 m from the edge of the stand. By the time focal observations began, many territories had already been delineated by spot mapping done during a different phase of this study (see section 2.2.1, above). Focal sessions began between 0530 and 1030 hr and were conducted between 23 May and 30 July, 1999. After arriving at the predetermined location, the observer quietly waited for approximately 15 min to allow birds to settle before beginning. The focal session began when a bird within 50 m first vocalized after the initial 15 min settling period. All vocalizations identified as songs were recorded in a hand-held voice recorder with a continuous time counter. Each song (or partial song) was tallied as a single occurrence. We made no attempt to distinguish between song types since song-type data typically is not collected during point-count surveys. Each bird was identified by number and tracked aurally, and visually were possible, as it moved about the area, even if it moved farther than 50 m away.

5.2. Variable Computation and Data Analysis

For each bird heard during a focal session, we calculated the total number of songs in 30 min (song count), songs per min for each of the 30 min (song rate), variance and coefficient of variation (CV) of song rate based on those 30, 1-min counts, number of min out of 30 that the focal bird sang at least once (singing duration). In conjunction with data from the spot mapping and nest searching phase of this study (see above), where possible, we ascribed territory status (territory holder versus no territory), mating status (mated versus not mated), breeding status (active or not active), nesting stage (no activity, nest building, eggs present, nestlings present, and complete), and nest fate (successful [i.e., one or more fledglings] versus failed) for each bird recorded in the focal session. We achieved this by matching the precise physical location of the focal observer (an x-y coordinate within pre-existing spot-mapping grids; see section 2.2.1., above) with known territories previously delineated for that same location by other field workers. If the focal observer was centered within a bird's territory during focal observations, we assumed that the "focal bird" was the holder of that territory. Because the observer also recorded the direction (compass bearing) and estimated distance (m) to counter-singing males from peripheral territories, we could identify those males as well and assign them to their own territories based upon existing territory maps. When the observer was positioned in-between two adjacent territories, we used the information recorded on direction and distance to focal males to assign birds to territories.

To ascribe territory status, mating status, breeding status, nesting stage, and nest fate for each bird recorded in focal sessions, we used the following criteria. Focal birds were considered territory holders if they were recorded singing within a known territory; if no territory had previously been delineated in an area where focal observations were conducted (which happened occasionally as focal birds were sometimes observed opportunistically), such focal birds were deemed to be without a territory. For focal males assigned to a territory for which other field personnel had found a nest during the ongoing nest monitoring component of this study (see section 3.3.1., above), we considered them to be mated; observed male-female pair-bond interactions (e.g., copulations, food-sharing, courtship displays) made by the focal observer also were taken as evidence that a male was mated. Non-territory holders and territorial males for which we had no evidence of nesting and/or interactions with females were assumed to be unmated. Breeding status was determined by comparing the dates on which focal observations were made with the known nesting phenology of birds for which we had found nests. Hence, if focal observations were made during the nest-building, egg-laying, incubation, or nestling stages of a nest to which the focal bird was assigned, we recorded the breeding status of that focal bird as "active." An "inactive" breeding classification was given to a bird if: (1) it was deemed non-territorial;

(2) it was considered territorial, but unmated; or (3) focal observations were made after the bird's nest had either successfully fledged young or had failed. Nesting stage also was determined by examination of the dates on which data were collected. The nesting stage of focal birds that had not started nesting at the time focal observations were made was considered as "no activity." Birds observed during an active part of the nesting cycle were recorded as such (i.e., "nest building," "eggs present," or "nestlings present"). The nesting stage of birds observed after the nest had successfully fledged young or had failed was considered "completed." Finally, the ultimate fate of a nest, if one was found for a focal bird, was used to assign nest fate as successful or failed, regardless of the date that focal observations were conducted.

While we had intended to collect information on movement rates and energy budgets of focal species, we found that one person could not collect reliable singing and movement data simultaneously. In some instances, the observer was recording vocalizations on up to seven individual birds as they were moving about the area, which precluded the opportunity to follow and locate individual birds during each movement.

Because this was a preliminary study, we explored the data in a variety of ways using an assortment of techniques. For example, we examined the focal observation data in terms of song counts (or rates) and singing durations because the relationship between detectability of birds and these measures is not completely clear (Wilson and Bart 1985). Despite the fact that in some cases these techniques may seem duplicative, we include them in an effort to be thorough.

We conducted two sets of analyses, one for each of the two focal species (i.e., Winter Wren and Song Sparrow). Each species was analyzed in the same way except where noted in the text. We examined scatterplots of all pairs of continuous variables, first using pooled data from all stands (pooled data; $n = 4$ for Winter Wren and $n = 2$ for Song Sparrow) and then by using stand-level data. Spearman rank correlation coefficient matrices for Julian date, time (start of focal session), total number of birds detected during a focal session, song rate, variance and CV of song rate, and singing duration for each species were generated to determine the strength of relationships between pairs of variables across all stands combined. We only report stand-specific results when they were different from results of pooled data. Unlike earlier sections of this report, here we use $\alpha = 0.05$ to interpret the significance of statistical tests.

We also conducted a series Kruskal-Wallis nonparametric tests on pooled data to determine if song rate was significantly related to categorical variables describing breeding activity (i.e., territory status, mate status, breeding status, nest fate, and nest stage). The Kruskal-Wallis test is the nonparametric analog of analysis of variance (ANOVA) for multiple groups (Kruskal-Wallis 1952, Zar 1996). When there are only two groups (e.g., territorial versus nonterritorial), the Kruskal-Wallis reduces to the Mann-Whitney test (Zar 1996). The intent of this exploratory analysis was to help determine sources of variation in song rate related to breeding activity rather than treatment effects *per se*. Measures of breeding activities were not independent of one another. For example, all mated Winter Wrens (n = 60), and all active breeders, were a subset of territorial individuals. Nonetheless, by conducting a series of nonparametric analyses and looking at each variable separately, we could examine *P*-values and determine which breeding activity might best explain variation in song rate across the entire data set.

Contingency table analyses, using Pearson Chi-square with Yates correction for continuity or Fisher exact test on 2 x 2 tables, were used to determine if the number of individuals by breeding activity (territorial, mating status, breeding status, and nest fate) made up the same proportion of the total number of birds in each stand. In combination with information on the relationship between song rates and breeding activity, contingency table analyses can help reveal sources of variation in song rates before testing for differences in song rates between treatments. Sample sizes were too small (i.e., more than 20% of the cells had counts less than five) to test for equality of proportions by nest stage for either species (Zar 1996)

The log-likelihood ratio was used to determine if the frequency distribution of Winter Wren singing durations, and if the frequency distribution of Winter Wren song counts were the same for stands within a treatment. When there was no significant difference between stands within a treatment, data from those stands were pooled and treatments were compared. Since the exploratory analysis suggested that song rate was related to territory status and that the proportion of territorial birds was not equal among stands, we repeated the log-likelihood test for only territorial wrens using the same procedures. This approach can help distinguish between differences in song rate related to differences in nesting phenology. Because Song Sparrow data was limited to two clearcuts and to few observations (n = 7 birds) in one of those two stands, distributions of Song Sparrow singing duration and song counts (for all individuals) were made for illustrative purposes only.

5.2.1. ***Analyses of variance*** - Before using parametric statistics, we tested song rate data for normality using the Kolmogorov-Smirnov test. We met normality assumptions for both focal species' song rate data by using the square root transformations (Zar 1996). We conducted a series of ANOVAs on Winter Wren song data to determine if square root of song rates (hereafter song rates) were different between stands within treatments and between treatments. First, in an attempt to understand which variables covaried with song rate, we conducted a series of univariate ANOVAs with song rate (pooled data) as the dependent variable and territory status, mating status, and breeding status, in turn, as the independent variable. The *F*-statistic for these tests was used to determine the order of entry (high to low) into a stepwise regression model designed to select the best covariates of song rate to be used in a final model to test for differences in song rates between stands and treatments. We used only territory, mating, and breeding status as potential covariates because: (1) we had nest stage and nest fate information for less than half (*n* = 49) of the wrens in the study; (2) nest stage and nest fate data were available only for the subset of wrens with territories; and (3) we found no relationship between song rate and nest stage or nest fate in our exploratory analysis described above. An *F* statistic probability of 0.15 was used to enter or remove independent variables from the model. The significant independent variable identified in the stepwise regression (i.e., territory status) was used as a covariate in an ANCOVA to test for differences in song rates among stands and between treatments. That is, song rate was the dependent variable, stand and treatment were independent variables, and territory status was the covariate. Because of the preliminary nature of this study, we tested for difference in song rates among stands and between treatments with and without territory status as a covariate.

5.2.2. *Bootstrap analysis* - We determined the proportion of individuals detected each min in a focal session by dividing the number of unique individuals heard that min by the total number of unique birds heard singing at least once during the focal session. Thus for each 30-min focal session, we had 30, 1-min estimates of the proportion of birds heard each min. This proportion can be viewed as a measure of how well 1-min point counts measure the true population of wrens in a designated area, assuming wrens are not moving into or out of the survey area. A bootstrap analysis was conducted to determine the relationship between the error in the proportion of birds detected and the number of min used to estimate that proportion. We drew 1,000 bootstrap samples (with replacement) each of 2–30 min of proportion data for all individuals of the target species using Resample Stats (Bruce 1993). The width of the 95% confidence limits (upper CL–lower CL) from the resulting distributions was plotted against number of length of the survey session.

5.3. Results

5.3.1. *Winter Wren* - We conducted a total of 33, 30 min focal sessions (three in Deschutes, four in Johnson, 16 in Kirkland, and 10 in Nisqually; see Table 1) during which we recorded song data on 106 individual Winter Wrens (18 in Deschutes, 13 in Johnson, 54 in Kirkland, and 21 in Nisqually). Spearman correlation coefficients between song rates and date ($r = 0.175$, $P = 0.073$), and between song rate and time of day ($r = -0.157$, $P = 0.109$) were low, which suggested that sampling date and time of day did not systematically affect song rates (Table 21). Similarly, the total number of Winter Wrens detected per focal session was weakly associated with individual song rate ($r = 0.141$, $P = 0.150$) and individual singing duration ($r = 0.165$, $P = 0.091$; Table

Table 21. Spearman rank correlation coefficients for focal observation data on Winter Wrens (*n* = 106) in forests of the southwest Cascade Mountains of Washington, 1999. Birds/session is the number of birds detected in a 30-min focal session; Song rate is the rate of individual songs; Variance is variance of 30, 1-min song rates; CV is the coefficient of variation in song rate; and Singing duration is the number of min that individuals were heard at least once during 30 min. *P*-values are below the diagonal.

Variable	Julian date	Time	Birds/ session	Song rate	Variance	CV	Singing duration
Julian Date		0.067	0.354	0.175	0.102	0.024	0.193
Time	0.498		-0.293	-0.157	-0.156	-0.088	-0.165
Birds/session	0.000	0.002		0.141	0.108	-0.097	0.165
Song rate	0.073	0.109	0.150		0.909	0.097	0.970
Variance	0.295	0.111	0.150	0.000		0.384	0.819
CV	0.806	0.368	0.332	0.324	0.000		-0.037
Singing duration	0.476	0.090	0.091	0.000	0.000	0.707	

21). Wrens did not appear to sing more frequently, or for longer periods, in response to increasing numbers of singing birds in the immediate area. Song rates were significantly correlated with variance of song rate ($r = 0.909$, $P < 0.001$) and with singing duration ($r = 0.970$, $P < 0.001$; Table 21). Birds with higher song counts had higher variance in song rate/min (consistent with a Poisson distribution), higher rates of songs/min, and sang during more min than birds with lower song rates (Fig. 23). The number of birds per focal session was related to date ($r = 0.354$, $P < 0.001$) and time when focal session began ($r = -0.293$, $P = 0.002$; Table 21).

Spearman rank correlations at the stand level were consistent with coefficients for data pooled across all stands with the following exceptions. Date and birds/session was positively correlated ($r = 0.646$) in Kirkland and negatively correlated ($r = -0.731$) in Johnson.

Kruskal-Wallis nonparametric ANOVA on pooled Winter Wren data suggested that territory status was the best predictor of song rates (Mann-Whitney [MW] U = 1658, $P = 0.001$), while mate status was less important (MW $U = 1091.5$, $P = 0.066$). Breeding status (MW $U = 1004.5$, $P = 0.172$), nest stage (Kruskal-Wallis $H = 7.093$, $P =$ 0.131), and nest fate (MW $U = 389.5$, $P = 0.869$) were not important at all. Nest stage and fate information was based on small sample sizes (Zar 1996; Table 22), so results should be interpreted carefully.

Contingency table analysis indicated that territory holders did not make up the same proportion of birds ($\chi^2 = 20.51$, $df = 3$, $P < 0.001$) in the four stands during focal sessions (Table 22). In particular, all Nisqually wrens ($n = 21$) and 92% of wrens in Johnson ($n = 13$) were territorial during the survey period, whereas 54% of wrens in Deschutes ($n = 13$) and 48% of wrens in Kirkland ($n = 54$) were territorial. Similarly, the proportion of mated to unmated birds ($\chi^2 = 14.34$, $df = 3$, $P = 0.003$), the proportion of birds that successfully nested ($\chi^2 = 11.93$, $df = 3$, $P = 0.008$), and the proportion of birds by nest stage ($\chi^2 = 30.116$, $df = 12$, $P = 0.003$; Table 22) were not equal among the four stands.

Analysis of frequency distribution of all wren (with and without territories) data suggested that there was a significant difference in distributions of Winter Wren singing durations between thinned stands (Log Likelihood $\chi^2 = 6.91$, $df = 2$, $P = 0.032$) but not between old-growth stands (Log Likelihood $\chi^2 = 4.37$, $df = 2$, $P = 0.11$). In addition, there was a significant difference among the two thinned stands and the pooled old-growth stands (Log Likelihood $\chi^2 = 14.01$, $df = 4$, $P = 0.007$; Fig. 24). Mean singing duration for pooled old-growth stands was 10.53 (SE = 0.81) min versus 12.22 (2.04) min for Deschutes (thinned) and 7.07 (1.45) min for Johnson (thinned). In contrast to wrens in Deschutes and the old-growth treatment, wrens in Johnson never sang more than 20 out of 30 min (Fig. 24). There was no significant difference in the distribution of Winter Wren song counts between thinned stands (Log Likelihood $\chi^2 = 4.33$, $df = 2$, $P = 0.12$), or in song count between old-growth stands (Log Likelihood $\chi^2 = 4.38$, $df = 2$,

Figure 23. Singing duration and song rate as a function of total song count for Winter Wrens in the southwest Cascade Mountains of Washington, 1999. Data were pooled from two old-growth and two commercially thinned stands.

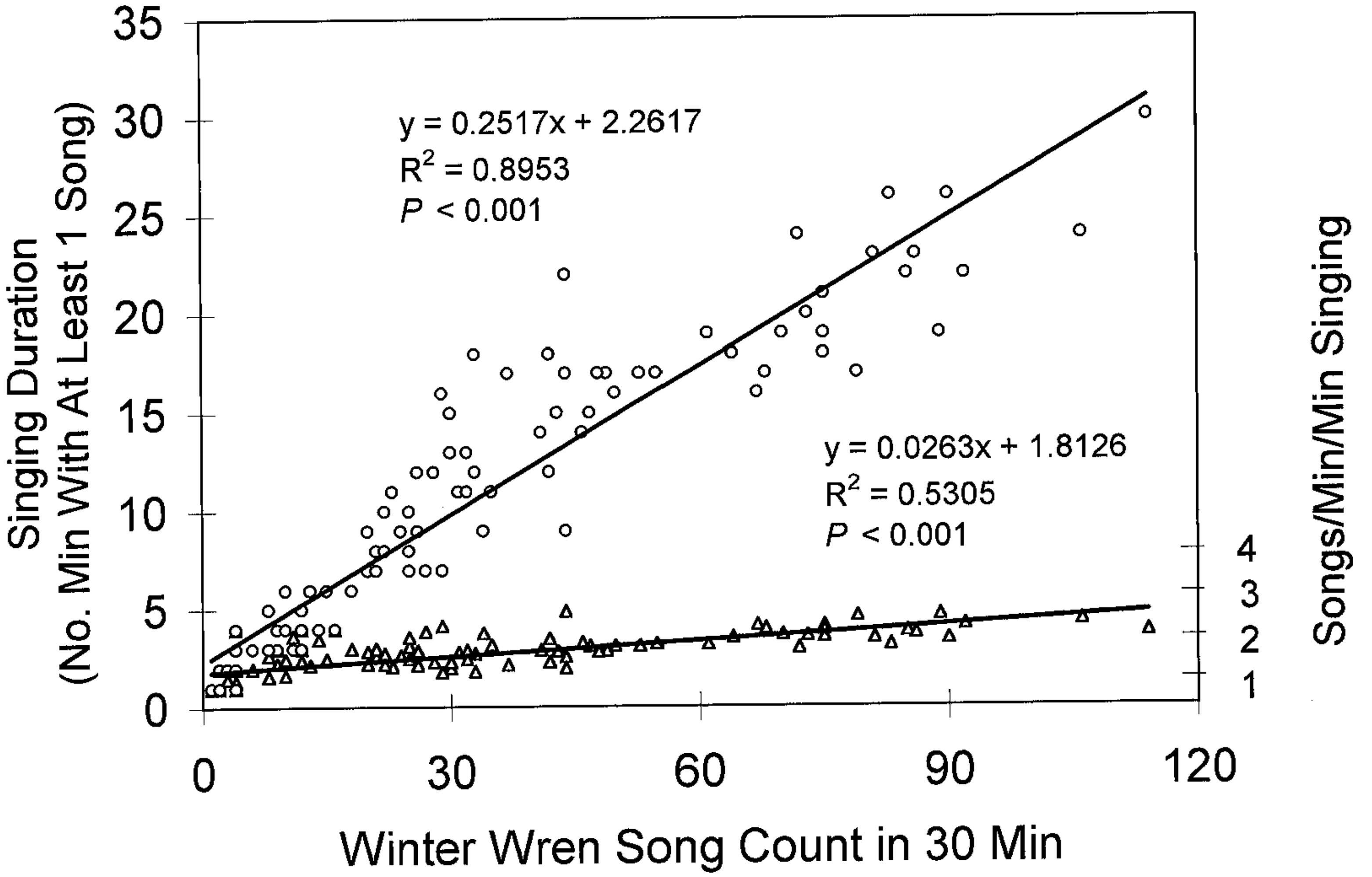
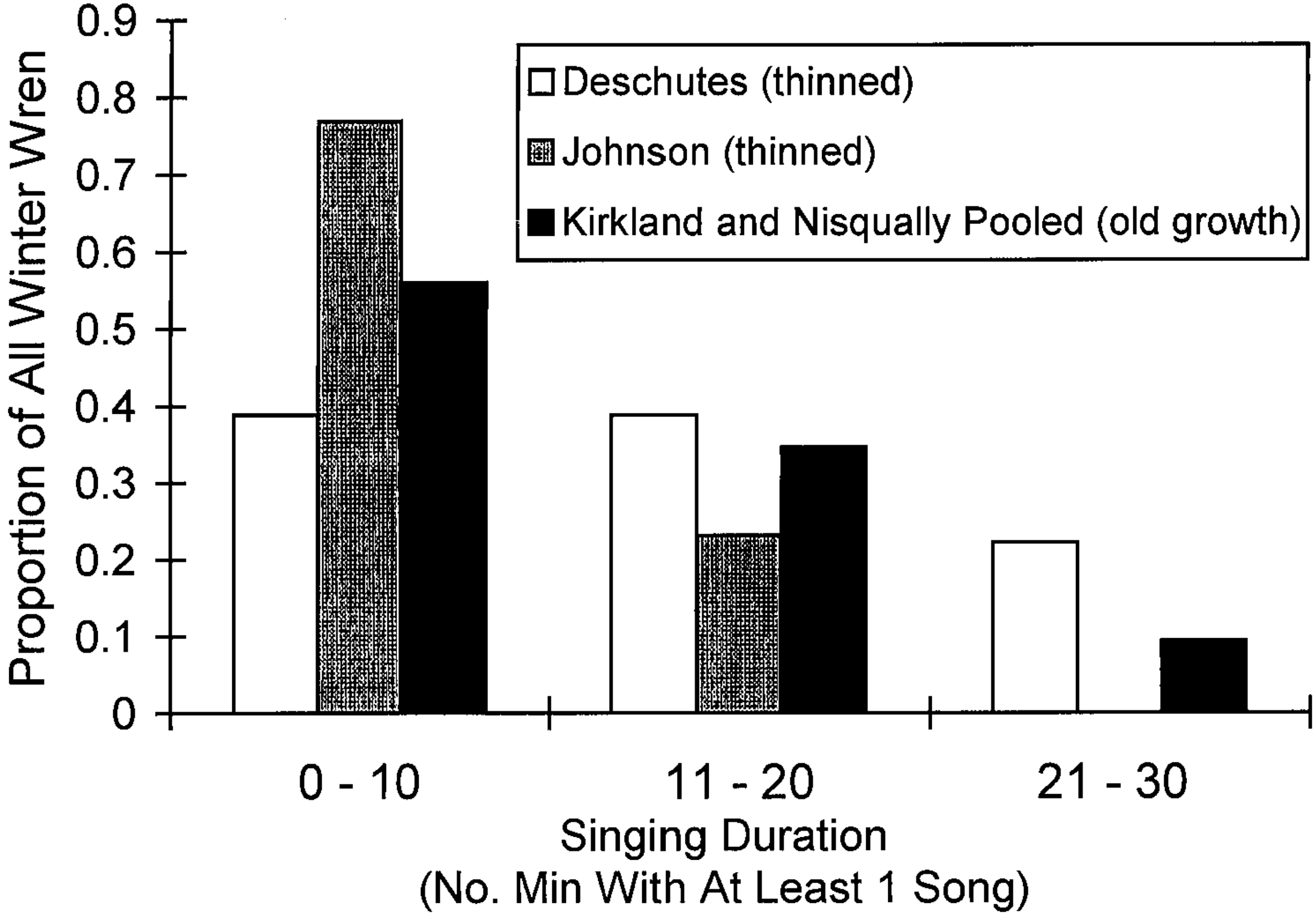


Table 22. **Number of Winter Wrens and Song Sparrows by territory status, mating status, breeding status, ultimate nest fate, and nest stage observed during focal observations in the southwest Cascade Mountains of Washington, 1999. Winter Wren data came from two stands in each of two treatments, old growth and commercially-thinned 60-year-old forests, and Song Sparrow data came from two clearcut harvest stands. Active breeding status means the individual was involved in nest building, egg laying, brooding, or feeding young. A successful nest produced one or more fledglings. Nest stage includes pre-nesting (pre), nest building (bld), egg(s) present (eggs), nestling(s) present (yng), and nesting completed (compl). Sample sizes for nest fate were relatively low because not all nests could be located. The proportion of Winter Wrens with territories ($P < 0.001$), with mates ($P = 0.008$), and that successfully nested ($P = 0.003$) was significantly different among stands.**

	Territorial		Mated		Breeding		Nest fate		Nest stage				
Stand	yes	no	yes	no	active	inactive	success	fail	pre	bld	eggs	yng	compl
Winter Wren - Old growth													
Kirkland	28	26	24	30	20	34	5	19	0	9	2	8	4
Nisqually	21	0	11	10	4	17	9	2	3	1	1	2	4
Winter Wren - Thinned													
Johnson	12	1	12	1	3	10	3	9	1	0	2	1	8
Deschutes	13	5	13	5	6	12	3	10	0	0	1	5	7
Song Sparrow - Clearcut													
O'Brian	28	5	13	20	4	29	8	5	0	1	9	3	0
Turner	5	2	5	2	2	5	1	4	0	0	3	0	2

Figure 24. Frequency distributions of all Winter Wren singing durations during 30-min focal sessions at four forest study plots in the southwest Cascade Mountains of Washington, 1999.



$P = 0.11$; Fig. 25). In addition, there was no difference in song counts between treatments (Log Likelihood $\chi^2 = 1.52$, $df = 2$, $P = 0.47$) after pooling song count data from stands within treatments. Wrens (with and without territories) sang an average of 31.15 (SE = 2.77) songs during focal sessions (Table 23).

When nonterritorial wrens were excluded from the analyses of frequency distributions, we found no significant difference in distributions of Winter Wren singing durations between thinned stands (Fisher Exact Test [Exact Test] $P = 0.434$) or between old-growth stands (Exact Test $P = 0.774$; Fig. 26). In addition, there was no significant difference in Winter Wren singing duration between pooled thin versus pooled old-growth stands (Log Likelihood $\chi^2 = 1.291$, $df = 2$, $P = 0.524$). The mean singing duration for all Winter Wrens with territories was 8.65 (SE = 0.80) min. Likewise, we found no significant differences in distribution of Winter Wren song counts between thinned stands (Exact Test $P = 0.411$), or between old-growth stands (Exact Test $P = 0.823$; Fig. 27). In addition, there was no significant difference in Winter Wren song counts between pooled thin versus pooled old-growth stands (Log Likelihood $\chi^2 = 1.084$, $df = 2$, $P = 0.582$).

Territory status was the only significant independent variable ($P = 0.001$) identified in the stepwise regression model (i.e., mate and breeding status were excluded from the final model). The final ANCOVA showed that there was no significant difference in song rate among stands ($F_{3, 101} = 0.28$, $P = 0.84$) and that territory status was a significant covariate of song rate ($F_{1, 101} = 8.25$, $P = 0.005$) although the model explained little overall variation in song rate ($R = 0.18$). Mean territorial Winter Wren song rate was 0.83 (SE = 0.10) songs/bird/min while nonterritorial Winter Wren song rate was 1.52 (0.18) songs/bird/min (Table 23).

5.3.2. *Bootstrapping analysis (Winter Wren)* - We had a total of 990 min focal session bird observations (33 focal sessions x 30 min/focal session). Precision of the estimate (as measured by width of the confidence limits) in bootstrap samples of those proportions decreases rapidly with increasing sample sizes and fits ($R^2 = 0.99$) a negative logarithmic function described by log(width of the CL) = -0.48*(length of survey) + log(1.21) (Fig. 28).

5.3.3. *Song Sparrow* - We conducted a total of 16, 30 min focal session (two in Turner and 14 in O'Brian; see Table 1) and recorded song data on 40 Song Sparrows (Table 22). Spearman correlation coefficients indicated weak relationships between song rate and date ($r = 0.135$), and between song rate and time of day ($r = 0.149$), suggesting that sampling date and time of day did not affect Song Sparrow song rates. Similarly, the total number of Song Sparrows detected per focal session was weakly associated with individual song rate ($r = 0.168$) and individual singing duration ($r = 0.137$). Song Sparrows did not appear to sing more frequently, or for longer periods, in response to

Figure 25. Frequency distributions of all Winter Wren song counts during 30-min focal sessions at four forest study plots in the southwest Cascade Mountains of Washington, 1999.

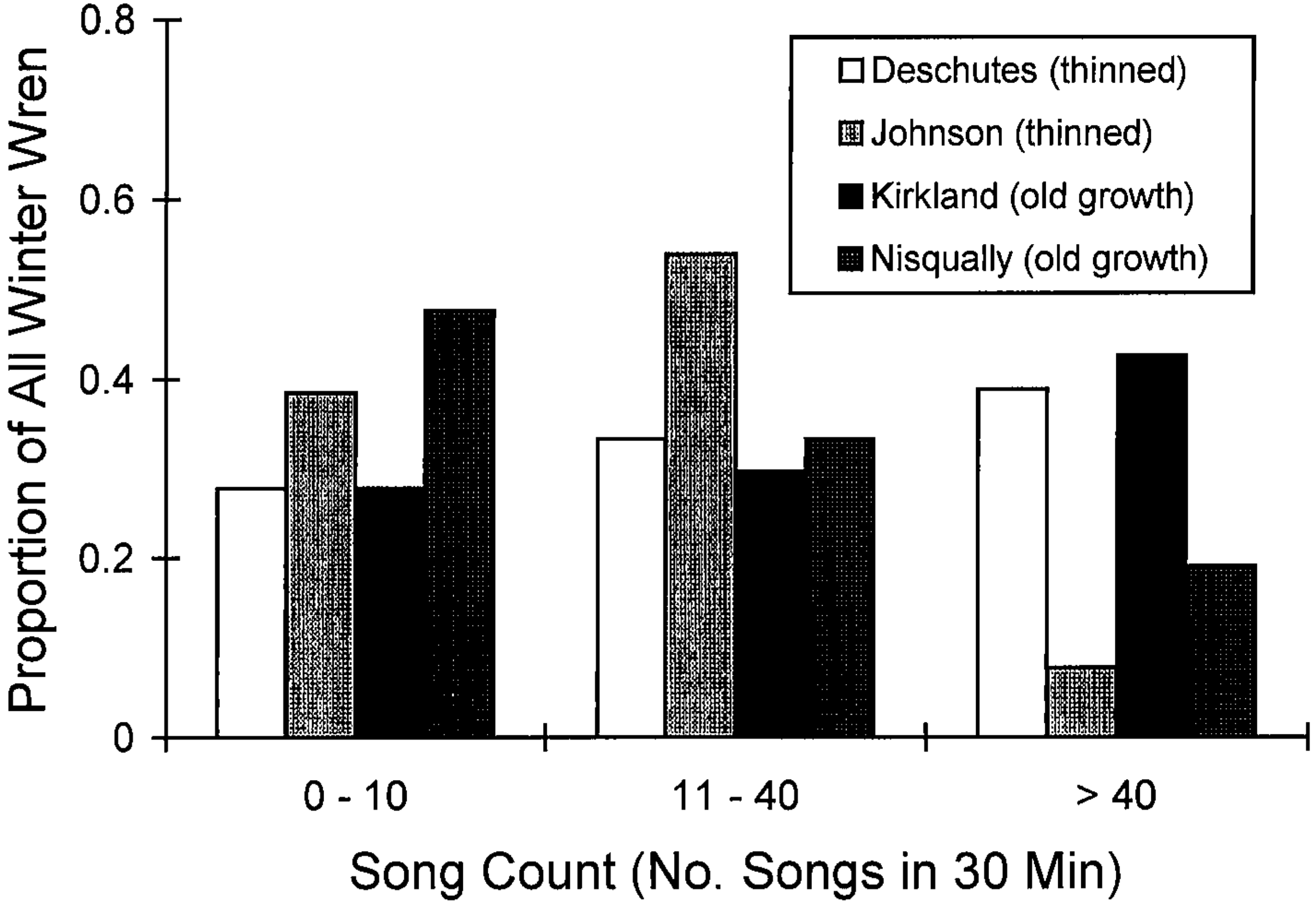


Table 23. Sample size, mean song rate (Song rate), and mean number of min individuals were heard at least once during 30 min (Singing duration) for territorial versus nonterritorial Winter Wrens in the southwest Cascade Mountains of Washington, 1999. Standard errors are in parentheses.

	Song rate				Singing duration	
	Territory		No territory		Territory	No territory
Stand	*n*	(songs/min/bird)	*n*	(songs/min/bird)	(min)	(min)
Old growth						
Kirkland	28	0.80 (0.15)	26	1.55 (0.20)	8.89 (1.36)	13.31 (1.43)
Nisqually	21	0.84 (0.22)	0	NA[a] (NA)	7.81 (1.62)	NA (NA)
Old-growth total	49	0.82 (0.13)	26	1.55 (0.20)	8.43 (1.03)	13.31 (1.43)
Thinned						
Johnson	12	0.68 (0.23)	1	1.13 (NA)	6.92 (1.57)	9.00 (NA)
Deschutes	13	1.03 (0.19)	5	1.46 (0.64)	11.08 (1.83)	15.20 (5.84)
Thinned total	25	0.85 (0.15)	6	1.40 (0.52)	9.01 (1.26)	14.17 (4.88)
Grand total	74	0.83 (0.10)	32	1.52 (0.18)	8.65 (0.80)	13.47 (1.43)

[a] Not applicable.

Figure 26. Frequency distributions of territorial Winter Wren singing durations during 30-min focal sessions at four forest study plots in the southwest Cascade Mountains of Washington, 1999.

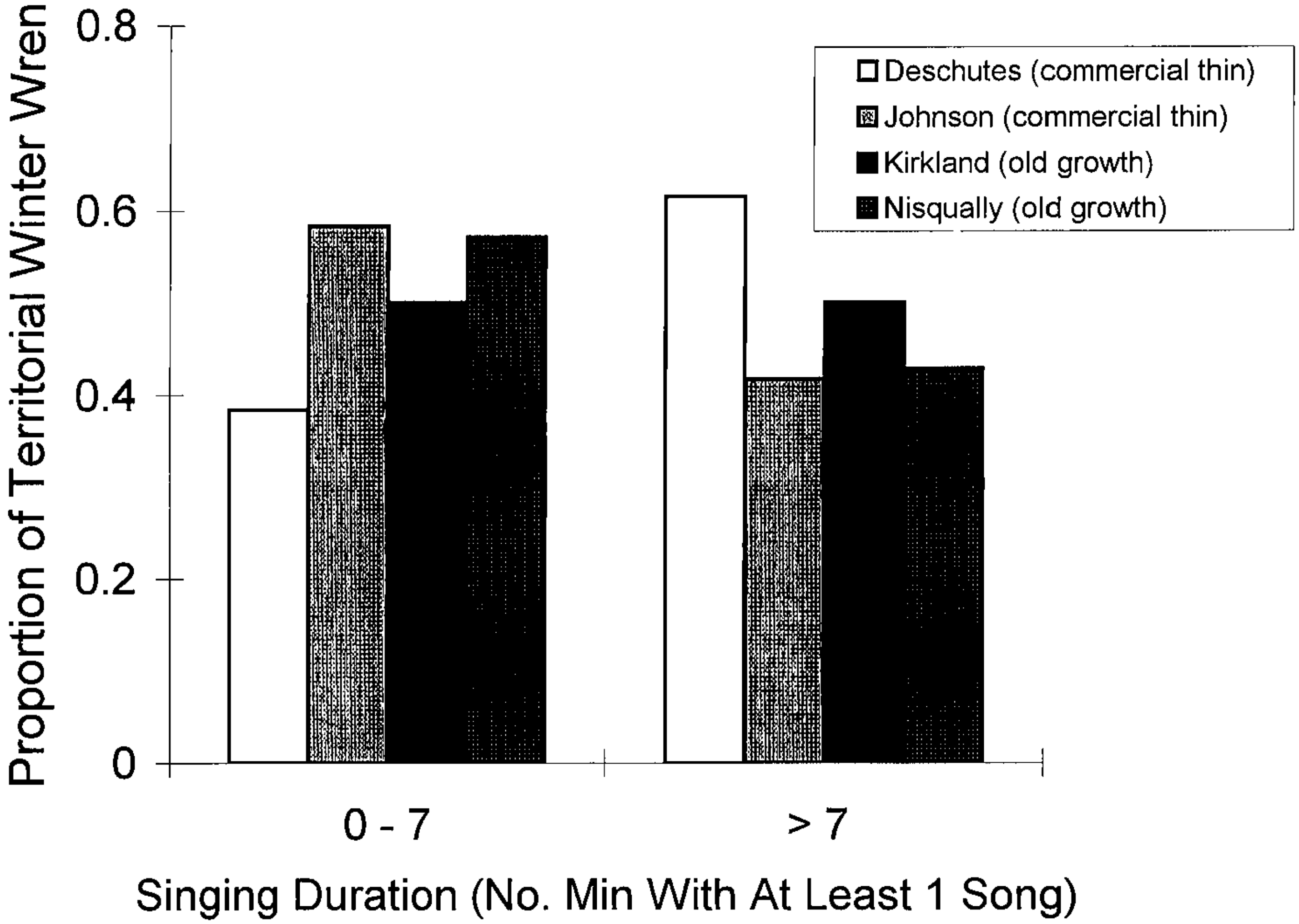


Figure 27. Frequency distributions of territorial Winter Wren song counts during 30-min focal sessions at four forest study plots in the southwest Cascade Mountains of Washington, 1999.

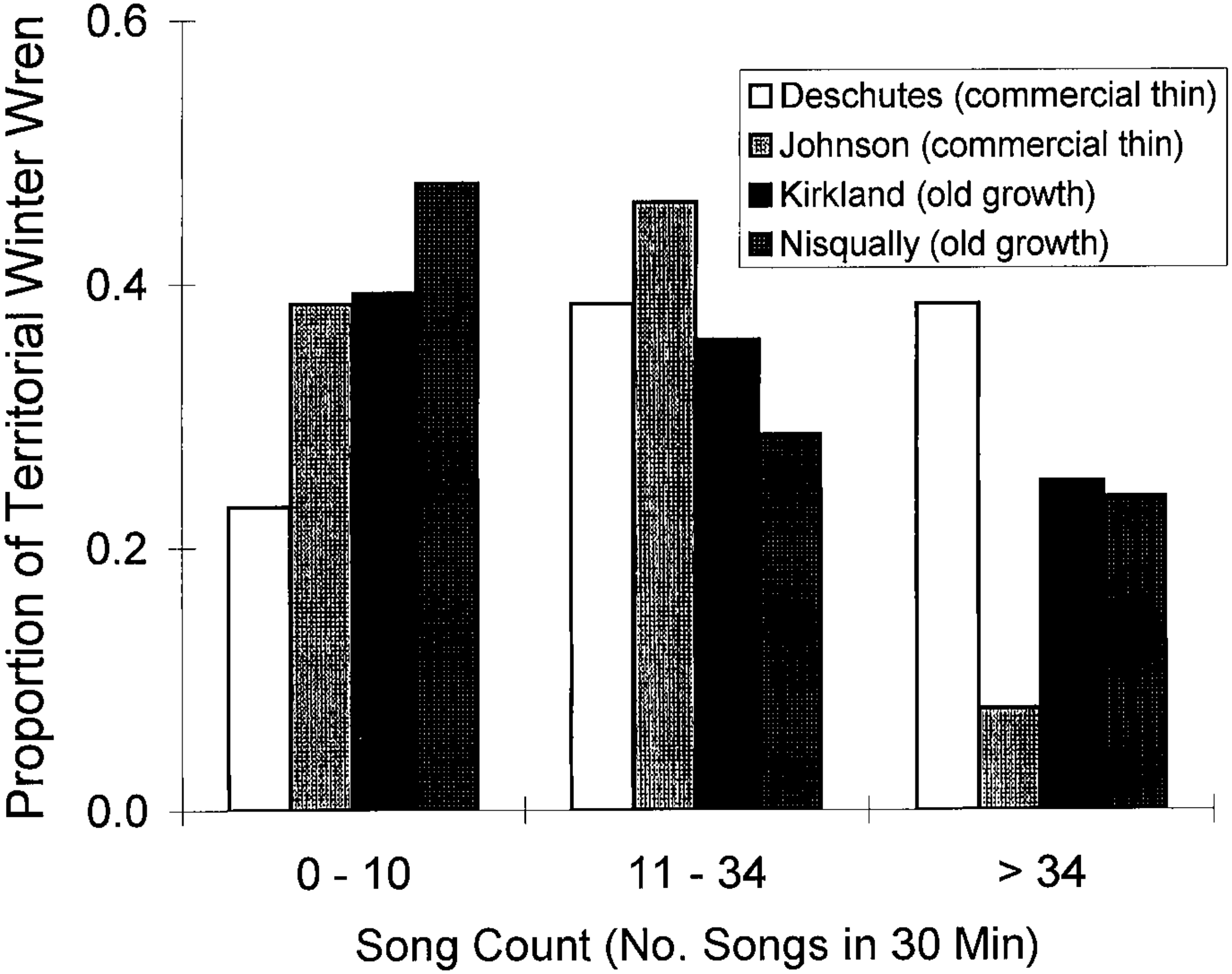
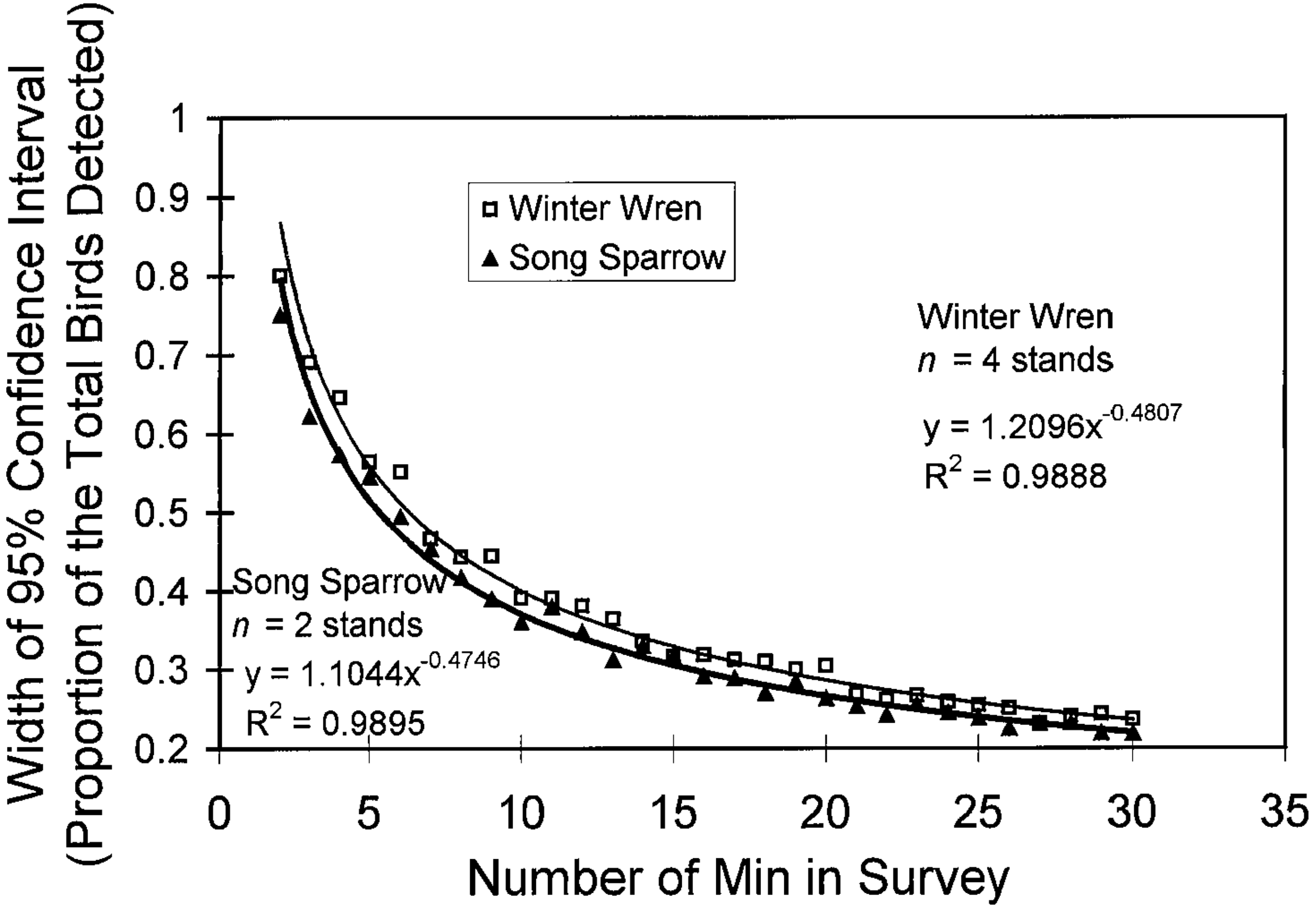


Figure 28. Precision, as measured by the width of the 95% confidence limits, of the proportion of birds[a] detected as a function of survey length during focal sessions in the southwest Cascade Mountains of Washington, 1999.



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[a] Proportion means and confidence limits were based on 1,000 bootstrap samples drawn with replacement from all 1-min estimates of the proportion of birds detected that min of a focal session.

increasing numbers of Song Sparrows in the immediate area. Song rates were significantly correlated with variance of song rate ($r = 0.927$, $\chi^2 = 37.53$, $df = 1$, $P < 0.001$) and with singing duration ($r = 0.964$, $\chi^2 = 96.22$, $df = 1$, $P < 0.001$; Table 24). Birds with relatively high song counts had higher rates of songs/min, higher variance in songs/min, and sang during more min than birds with lower song rates (Fig. 29). The number of birds per focal session was related to date ($r = 0.493$, $P = 0.001$; Table 21)

Kruskal-Wallis nonparametric ANOVAs on Song Sparrow pooled across stands suggested that territory status (MW $U = 75.5$, $P = 0.154$), mate status (MW $U = 209$, $P = 0.765$), and breeding status (MW $U = 110$, $P = 0.762$), were each relatively poor predictors of song rate. Contingency table analysis indicated that territorial Song Sparrows (Exact Test $P = 0.584$) made up the same proportion of total Song Sparrows in the two clearcut stands. Similarly, the proportions of mated to unmated birds, active to inactive nesters, and birds that successfully nested ($\chi^2 = 14.34$, $df = 3$, $P = 0.003$; Table 22) were the same across the two clearcut stands.

The distribution of Song Sparrow singing durations and song counts in clearcut stands appeared similar (Figs. 30 and 31, respectively). Mean Song Sparrow song rate was 0.84 (SE = 0.13) songs/bird/min and singing duration was 8.1 min (SE = 1.02). Like their nonparametric analogue, univariate ANOVAs suggested that territory status ($F_{1,38} = 2.24$, $P = 0.14$), mate status ($F_{1,38} = 0.03$, $P = 0.88$), and breeding status ($F_{1,38} = 0.04$, $P = 0.84$) were each relatively poor predictors of square root of song rate (hereafter song rate). Territory status was the only significant independent variable ($P = 0.14$) identified in the stepwise regression model to find the best predictor of song rate (i.e., mate and breeding status were excluded from the final model).

5.3.4. *Bootstrapping analysis (Song Sparrow)* - We had a total of 480 min focal sessions of bird observations (16 focal sessions x 30 min/focal session). Error (as measured by width of the confidence limits) in bootstrap samples of those proportions decreases rapidly with increasing sample sizes and fits ($R^2 = 0.99$) a negative logarithmic function described by log(width of the CL) = -0.47*(survey length) + log(1.10) (Fig. 26).

5.4. Discussion

We found significant differences between treatments in frequency distributions of all (territorial and nonterritorial) Winter Wren singing durations, which suggested that Winter Wrens were singing longer on average in some stands than others. However, these differences were not consistent with respect to treatment. Singing durations of Winter Wrens in pooled old-growth stands were intermediate relative to singing durations in two thinned stands (Fig. 24). Moreover, differences in singing duration

Table 24. Spearman rank correlation coefficients for focal observation data on Song Sparrows (*n* = 40) in the southwest Cascade Mountains of Washington, 1999. Birds/session is the number of birds detected in a 30-min focal session; Song rate is the rate of individual songs; Variance is variance of 30, 1-min song rates; CV is the coefficient of variation in song rate; and Singing duration is the number of min that individuals were heard at least once during 30 min. *P*-values are below the diagonal.

Variable	Julian date	Time	Birds/ session	Song rate	Variance	CV	Singing duration
Julian Date		-0.269	0.493	0.135	0.001	-0.235	0.201
Time	0.093		0.125	0.149	0.198	0.247	0.089
Birds/session	0.001	0.472		0.168	0.177	0.158	0.137
Song rate	0.407	0.376	0.299		0.927	0.476	0.964
Variance	0.997	0.228	0.276	0.000		0.731	0.832
CV	0.144	0.122	0.331	0.002	0.000		0.298
Singing duration	0.214	0.621	0.399	0.000	0.000	0.062	

Figure 29. Singing duration and song rate as a function of song counts for Song Sparrows during 30-min focal sessions in the southwest Cascade Mountains of Washington, 1999. Song Sparrow data are pooled from two clearcut stands.

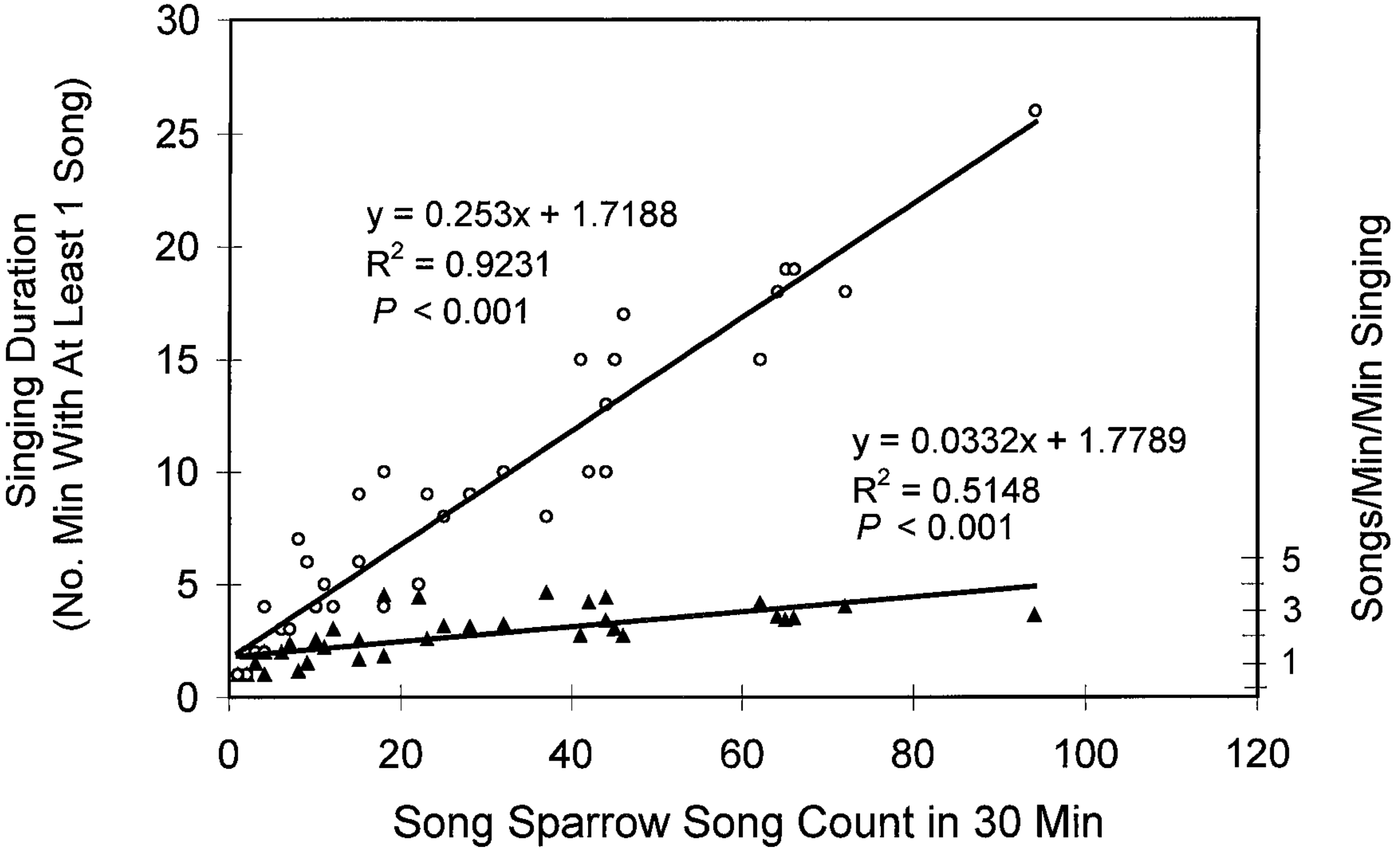


Figure 30. Frequency distributions of Song Sparrow singing durations during 30-min focal sessions at two clearcut stands in the southwest Cascade Mountains of Washington, 1999.

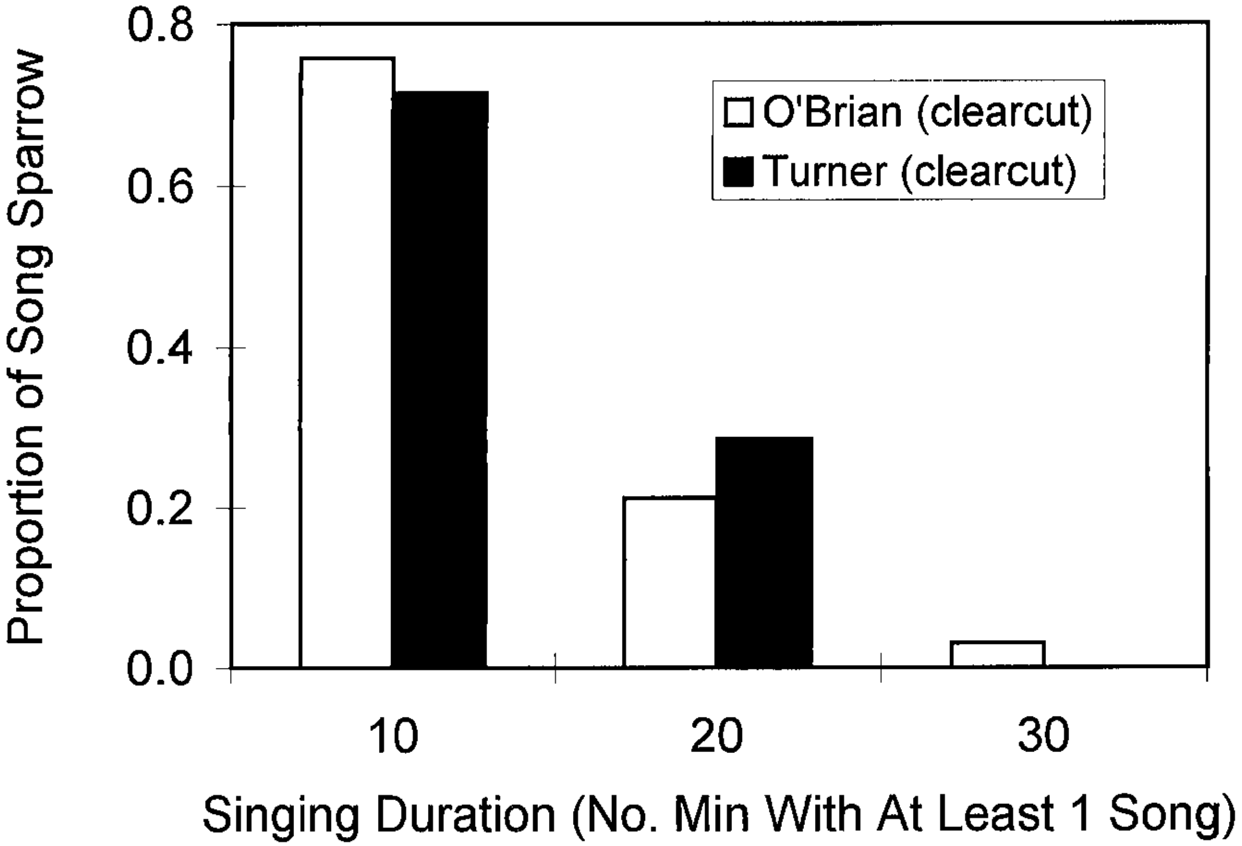
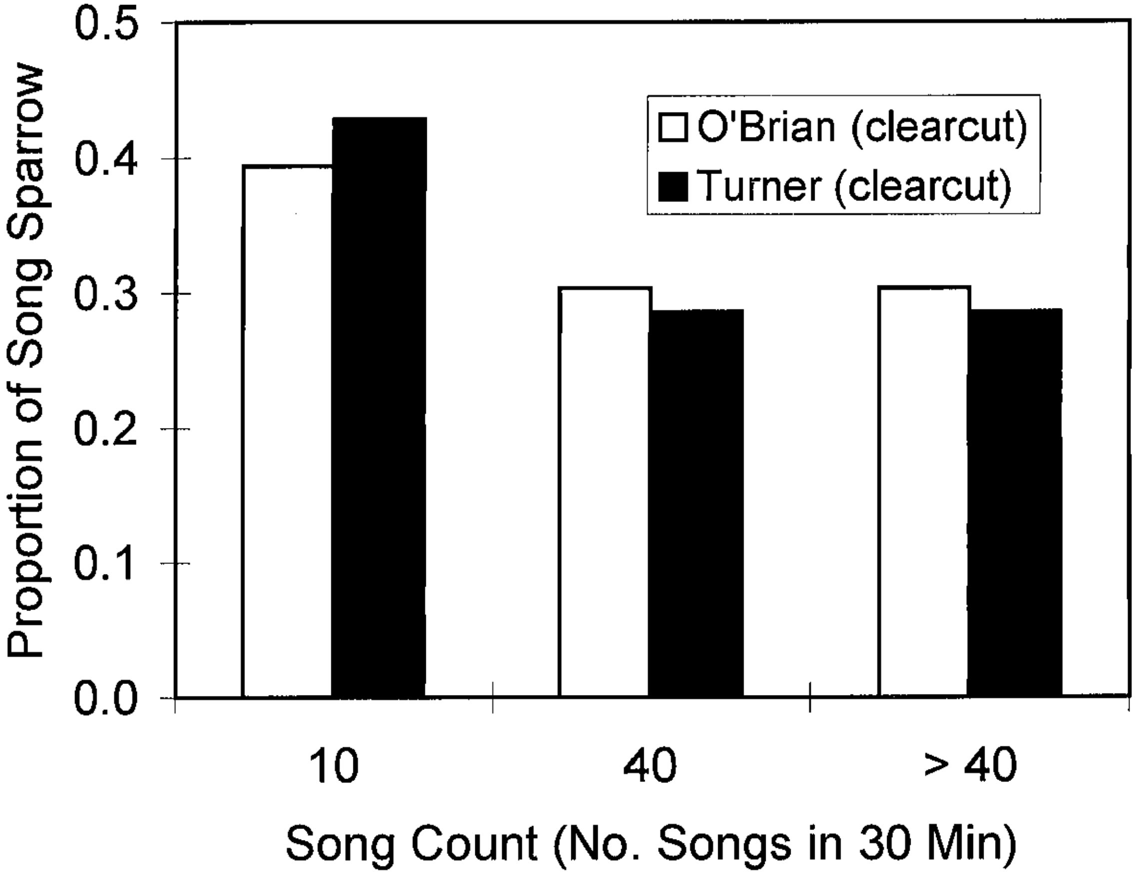


Figure 31. Frequency distributions of Song Sparrow song counts during 30-min focal sessions at two clearcut stands in the southwest Cascade Mountains of Washington, 1999.



were not apparent when nonterritorial wrens were removed from the analysis, and there were no differences in frequency distribution of song counts. This suggests that while there was a large variation within and between stands, especially thinned stands, there was no effect of treatment on Winter Wren vocalizations.

Variation in song count and singing duration among stands may have been due in part to differences in the ratio of territorial to nonterritorial wrens. Territorial wrens sing at approximately half the rate of nonterritorial wrens, and the ratio of territorial to nonterritorial wrens was different among stands during the focal study. We cannot explain why there were relatively high proportions of nonterritorial wrens during focal sessions in two of the four stands. With the exception of Deschutes, where three focal sessions occurred on the same day, focal sampling dates by stand were fairly evenly distributed across the late May–late July field season. That is, we found no relationships between song rate, and singing duration, and sampling date, and the number of birds per focal session was not strongly related to song rates or singing durations in either the Winter Wren or Song Sparrow. Furthermore, we found no evidence from spot-mapping data (see section 2.2.3., above) that the ratio of Winter Wren abundance (determined by point counts) to number of territories (determined from spot mapping) was different among stands. Such evidence would have supported the idea that some stands (Kirkland and Deschutes) had proportionately less territory holders than others over the course of the breeding season. We hypothesize that differences in nesting phenology, possibly related to stand elevation (at least in Kirkland), were responsible for differences in ratios of territorial to nonterritorial wrens. These differences were probably responsible for large variation in rates among stands and for the difference we found between old growth and thinned stands singing duration. Interestingly, Song Sparrow data suggests that variance between stands within a treatment can be quite small even with relatively small sample sizes.

The implication of our results on the accuracy of point count methodology to determine habitat quality is not entirely clear. Theoretically, detection of an individual could be influenced by both higher songs/min/min singing and by increased singing duration. While we have no data on how detectability changes with increasing songs/min singing, we showed how increasing the number of min in a survey (assuming that a bird can be detected after a single song) can decrease error associated with estimating the true number of birds in the survey area (see Fig. 4).

Our findings for Winter Wrens suggest that the main function of Winter Wren songs is territorial rather than mate attraction since song rate declines by approximately 50% after wrens establish a territory. This finding was consistent with Wilson and Bart's (1985) study of the House Wren, which showed a marked decrease in song rate with onset of mate acquisition and nesting activity. This finding also underscores the need for vocalization surveys over the full nesting period, especially if there are reasons to expect differences in nesting phenology (Lynch 1995). Song rates in territorial Song Sparrow tended to be higher (not statistically significant) than rates for nonterritorial Song Sparrows, which suggested that the function of songs is mate attraction rather territorial defense.

While territory status clearly affected song rates in Winter Wrens, mating status did not. Unfortunately, our data set was small, especially for some stands (e.g., Johnson and Deschutes) and conclusions about the effect of mating and nesting status suffer from our inability to unambiguously identify individual birds. Whereas establishing the nesting success of birds will always be time consuming, uniquely marking birds will help researchers understand vocalization characteristics as they relate to nesting phenology for a species. It could be that vocalizations during one part of the breeding season are better indicators of nesting success and thus habitat quality than others, with the added advantage that song counts could be done for shorter periods of time. The bootstrap analysis supports the idea that efficiency, defined as the decrease in variance per additional unit of survey time, changes as a negative logarithmic function. Variance in estimates of the proportion of birds detected (number detected/total number present) decreases at a decreasing rate with increasing survey time. With information on variance associated with increasing the number of point counts within a stand, variance associated with survey length could be used to determine efficient sampling schemes.

5.4.1. ***Management implications*** - The intent of this preliminary study was to determine if winter wren song count and singing duration (collectively referred to as song rate) varied by treatment, and secondarily by nesting and mating status. Treatment-level differences in song rate could result if alpha males establish territories in optimal habitat (treatment 1) and beta males are relegated to suboptimal habitat (treatment 2). Beta males, which may occur at relatively higher densities in suboptimal habitat (McShea and Rappole 1997), may sing more than alpha males in response to higher densities and presumably more encounters with conspecifics. In addition, beta males in suboptimal habitat may be less successful than alpha males at establishing territories and breeding, and thus sing more than mated alpha males as they constantly attempt to attract a mate (Krebs 1971). Differences in song rates presumably affect detection probability although the exact nature of the relationship is unknown. If detection probabilities are greater for beta males (because they sing more) than alpha males at the same density, then the assumption of equal detection probabilities by treatment is violated (Buckland et al. 1993) and suboptimal habitat might appear as having higher bird abundance than optimal habitat.

Our study suggested that winter wren song rates were not different between treatments although there was a great deal of variability within and between treatments. Taken alone, Winter Wren song data suggested that old-growth and commercial thinned stands do not represent optimal versus suboptimal habitat, and/or that Winter

Wrens do not exhibit territorial or behavioral hierarchies manifested by changes in song rates. We conclude that point counts, as applied to Winter Wrens in these two treatments, were not an inherently biased survey method for determining relative abundance, since vocalization rates and presumably detectability of birds, was the same between treatments.

Researchers may be able to devise new ways of assessing bird habitat quality by knowing how vocalization rates change as a function habitat quality or nesting and breeding status. For example, if per-capita song rate is higher in stands with low habitat quality (for any reason), then counting songs per bird may be more efficient than counting the total number of birds. There are other practical implications as well. It may be that song counts at certain times of the breeding season (e.g., after most territories are established) are better indicators (higher correlations) with abundance than song counts averaged throughout the season. Given that non-territorial Winter Wren song rate is twice the rate of territorial Winter Wren, using pre-territorial song count data may introduce unnecessary variance in song count data.

Point counts offer a relatively inexpensive way to survey many species of forest birds. We encourage others to critically examine the relationship between song rates and reproductive success of birds in forests of the Pacific Northwest so that we can improve point-count methods while better understanding their limitations.

6. Habitat Data

In addition to all bird data so far reported on here, we also collected the following habitat (vegetation) data in all 12 study plots: (1) data to characterize the structure and composition of study plots (stand-level data); and (2) data to describe the habitat characteristics around nests of selected species (nest-level data). In this report, we summarize stand-level habitat data in Appendices 3–8, but do not expose them to statistical analyses or use them to generate models of bird-habitat relationships. Although important, such analyses do not directly address the primary study objective of understanding how abundance and density are related to reproduction, and are therefore considered beyond the scope of this report. Nest-level habitat data, collected at a combined total of 125 nests, are not reported.

6.1. Measuring Forest Habitat

6.1.1. ***Field protocols (stand-level sampling)*** - Intensive sampling of forest structural attributes and vegetation composition occurred systematically throughout all 12 study plots (six in 1998 and six in 1999). Protocols followed those of Aubry et al. (1997) and

Hallett and O'Connell (1997), with a few modifications from Sallabanks (1994, 1995). Our protocols yielded the same suite of habitat variables described in previous studies of wildlife-habitat relationships in the state of Washington. Modifications included the following: (1) measuring canopy height from the bottom of the live crown (using clinometers), in addition to tree height (i.e., height to the top of the crown); (2) measuring the DBH of all snags, as well as height and decay class; (3) recording plant association (habitat type) using Chappell et al. (*in prep.*); and (4) conducting ocular estimates of percent cover for all major ground cover types (see Aubry et al. 1997) within a 2-m radius circle centered on the point-count station or nest. See Appendices 3–8 for summary statistics of the predominant structural variables such as ground cover types, tree species composition, density, and diameter, forbs, shrubs, and canopy cover and canopy height.

6.1.2. ***Field protocols (nest-level sampling)*** - In 1998, additional microhabitat sampling also occurred at and around the nest site for the following species: Winter Wren (*n* = 23 nests), Dark-eyed Junco (*n* = 15 nests), and American Robin (*n* = 9 nests). In 1999, Song Sparrow and Pacific-slope Flycatcher were added to this list, with all data being collected following suggested BBIRD protocols (Winter Wren, *n* = 32 nests; Dark-eyed Junco, *n* = 9 nests; American Robin, *n* = 5 nests; Song Sparrow, *n* = 26 nests; and Pacific-slope Flycatcher, *n* = 6 nests). These data were intended to be species-specific and extrapolation to other species has not occurred. Microhabitat data collected at the nest, when compared with the same data collected at random sites away from the nest but within the study stand (e.g., at point-count stations; see section 6.1.1., above and Appendices 3–8), will help identify important features of nest-site selection (i.e., habitat selection within stands at very small spatial scales). Moreover, microhabitat characteristics can be compared between successful and failed nests to examine the possible influence of microhabitat, and other spatial considerations (e.g., distance to edge or opening) on reproductive success. In 1998, nest-site microhabitat sampling also included the collection of data on relative humidity and temperature at some nests.

7. Key Findings and Suggestions for Future Research

7.1. Key Findings

What are the relationships between relative avian abundance and density as derived from traditional point-count survey and spot-mapping techniques, respectively, and how do these parameters correlate with habitat quality as measured by reproductive success?

- For many species it appeared that relative abundance, as derived from point counts at 50–100 m radii, was a reliable indicator of territory density and thus habitat quality, because for most species there was little evidence of density-dependent fledging rates. In other words, higher abundance translated into more territories, which in turn meant more young produced per unit area. Furthermore, for these species, an increase or decrease in abundance across a range of forest conditions appeared to mean the same thing relative to habitat quality.

- Species for which we observed density independent per-capita reproduction were the American Robin, Brown Creeper, Dark-eyed Junco, Orange-crowned Warbler, Song Sparrow, and Spotted Towhee. Species for which we observed inversely density dependent per-capita reproduction were the Willow Flycatcher and Winter Wren. For all of these species, therefore, we conclude that relative abundance, as derived from point counts at 50–100 m radii, was a reliable indicator of habitat quality.

- Regardless of which density measure we used (i.e., that derived from spot mapping or that derived from DISTANCE software), the correlation with relative avian abundance sampled at small detection distances (i.e., 15- and 25-m point-count radii) tended to be low and highly variable.

- For species with density dependent per-capita reproduction (i.e., nest-level productivity and/or Mayfield nest success), measures of abundance from point-count surveys would not be reliable indicators of habitat quality. In our analyses, those species were Chestnut-backed Chickadee, Varied Thrush, and Pacific-slope Flycatcher.

- Correlation analyses among abundance, density, and area-level productivity suggested that habitat quality could be reliably inferred from point-count surveys or assessments of density for six of 11 species examined (Brown Creeper, Chestnut-backed Chickadee, Dark-eyed Junco, Song Sparrow, Willow Flycatcher, and Winter Wren). Of the five species for which area-level productivity was uncorrelated with abundance and density (American Robin, Orange-crowned Warbler, Spotted Towhee, Varied Thrush, and Pacific-slope Flycatcher), the Varied Thrush and Pacific-slope Flycatcher had very low correlations; it is for these two species in particular, therefore, that we question the reliability of survey-type data for habitat quality assessments.

- We found no significant negative correlations between area-level productivity and either relative avian abundance or density estimates from spot mapping for any bird species. This is somewhat reassuring because if we had, such a result would have suggested that survey data were highly misleading, inferring that the lowest quality habitat was in fact the highest, and vice versa.

- The relatively high correlation between area-level productivity and density for many species provides evidence in support of the notion that density derived from spot mapping is a better index of habitat quality compared with relative abundance derived from point counts. Although more time-consuming, therefore, our data suggest that in lieu of finding nests, researchers may better assess habitat quality by mapping territories than by conducting point counts.

Based upon meta-analyses of data collected in forest types of the southwest Cascade Mountains of Washington, as well as elsewhere in the PNW (east-central Washington, northeast Oregon, and west-central Idaho), for which species (or species' guilds) is relative abundance likely to be a misleading indicator of habitat quality?

- Our analyses of treatment-level effects imply that many birds on point counts in one forest treatment means something very different from many birds on point counts in another forest treatment. At best, this means that habitat quality can only be assessed in relative terms when comparing treatments, and at worst, that increased abundance means something different entirely, perhaps even the opposite of what seems intuitive.

- The only species for which we found the relationship between area-level productivity and relative abundance to differ significantly ($P = 0.10$) between forest treatments was the Winter Wren. For this species, point counts were significantly positively correlated with habitat quality in old-growth forest, but uncorrelated in commercially-thinned forest.

- Meta-analyses of data from four regions of the Pacific Northwest were somewhat ambiguous, revealing few statistically significant results. We found little evidence to suggest that survey data could not be used to infer habitat quality for the majority of species or species' groups across the Northwest, but did find some exceptions, as well as some that were dependent on region and harvest intensity. We also found that quality of habitat, as measured by nest success and productivity, was fairly consistent among regions.

What are the relationships between breeding and mating status on song rates in both the Winter Wren and Song Sparrow, and how do Winter Wren song rates vary with forest type per se*?*

- The vocalization study suggested that while Winter Wren vocalization rates (singing duration and song counts) can be quite variable, there was little evidence to suggest that those rates varied by treatment type. The best predictor of song rate by Winter Wrens and Song Sparrows was territory status, although the two species showed opposite patterns.

7.2. Suggestions for Future Research

- For many species studied here, point counts were positively correlated with territory density. In addition, there appeared to be no density dependency in fledging rates for most species. Given that, it seems that knowing the reproductive contribution of floaters (nests not associated with territories) is critical to understanding how productive an area truly is. We believe that this research could best be accomplished by studying individually-marked birds throughout the breeding season in an extension of the pilot focal observations study reported on here.

- It has been suggested that territoriality helps regulate populations in the sense that territory holders become reproductive winners and nonterritory holders losers. For several presumably territorial species, we found density dependent fledging rates, which may suggest that that some resource in the forest is limiting (other than the numbers of territories that can fit into an area). We believe that future research could be focused on identifying: (1) if there were differences in density dependency between forest treatments of species we identified in this study; and (2) if there were differences, how forest management *per se* could explain those differences.

- The ultimate measure of habitat quality is fitness, of which reproductive success is just one component. Survivorship and reproductive life-span also are major components of fitness but were beyond the scope of the study we report on here. To better measure fitness, therefore, future studies might strive to estimate λ, the finite rate of population change. Estimating λ uses both age-specific fecundity and survivorship parameters and would require knowledge of adult and juvenile mortality rates, return rates (annual survivorship) of individually-marked birds, and the number of female offspring produced per adult female that survive to reproduce themselves.

- Song rate is clearly a function of nesting phenology and territory status, but these sources of variation are rarely controlled for in forest-bird studies. Researchers often assume that spreading visits across the breeding season is adequate to control for differences in nesting phenology. We therefore believe that we need better data on vocalization rates across the breeding season. This research is important because it would help us better control for song variation within a forest stand, and may lead to more accurate interpretations of data from point-count surveys.

- Our inferences about the potential effects of forest treatment on the relationship between abundance and reproduction were hindered by small sample sizes and low statistical power. Future work designed to address such effects should increase replication of the forest treatment types, perhaps to as many as 8–10 replicate stands per treatment. Such research would also benefit from including closed-canopy forests between 12 and 40 years old. This age class was not included in our study yet currently dominates many managed forest landscapes; in the future, as we possibly move into short-rotation plantations, 12–40 year-old forest will become even more abundant over space and time.

- Songbird population dynamics are difficult to understand using only two-years worth of data. Most passerines live beyond two years of age and annual variation in environmental factors (e.g., weather) can be high. To make more meaningful inferences about songbird population "viability", therefore, we recommend that future studies consider monitoring between three and five breeding cycles.

8. Acknowledgments

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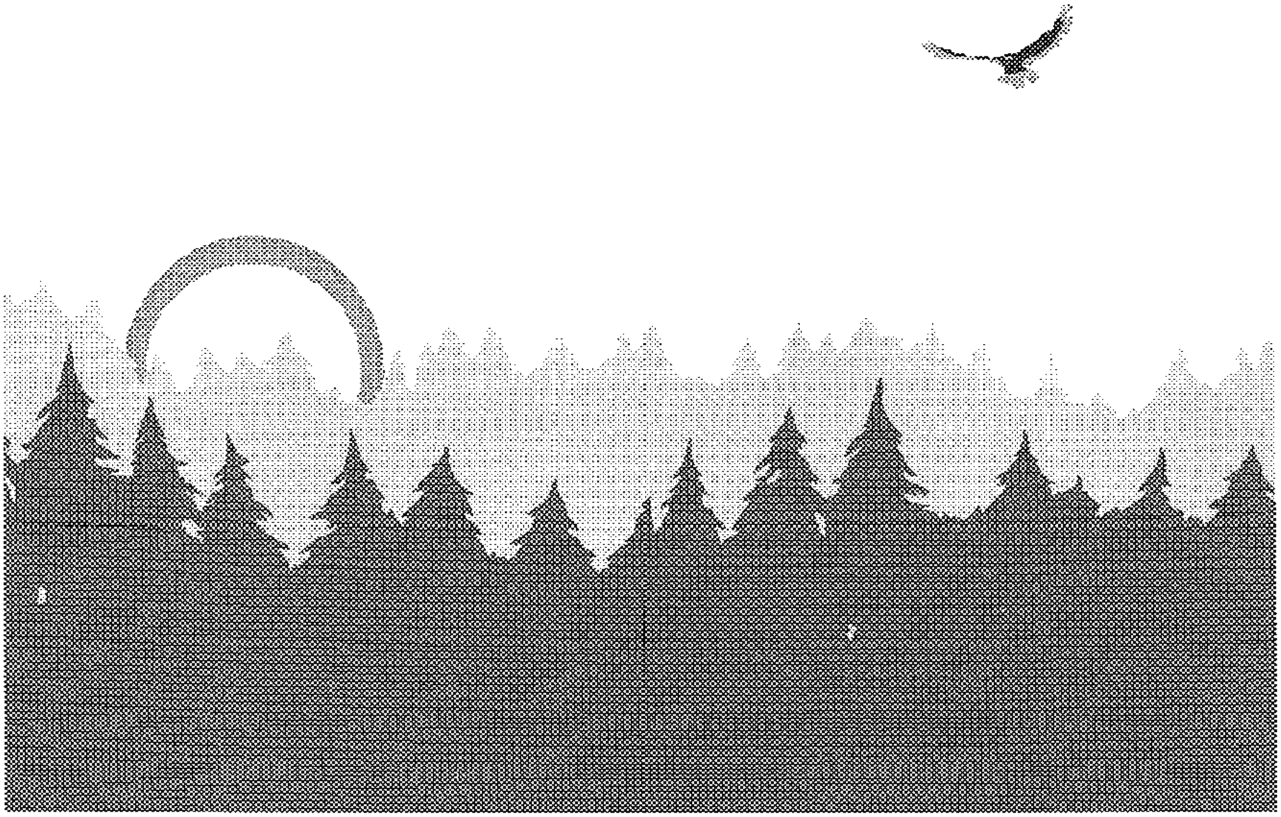

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Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
American Robin	Clearcut	Treatment	GALL 98	0.14754	0.066555	0.32708	0.4235	125
			GALL 99	0.5164	0.32136	0.82981	0.2456	125
			MINE 98	0.17213	0.081696	0.36268	0.3944	125
			MINE 99	0.22131	0.11329	0.43233	0.3519	125
			OBRI 98	0.27049	0.14618	0.50052	0.3219	125
			OBRI 99	0.56558	0.35768	0.89431	0.237	125
			TURN 98	0.54099	0.33949	0.8621	0.2411	125
			TURN 99	0.68853	0.44962	1.0544	0.22	125
	Comm Thin	Stand	DESC 98	0.46685	0.33056	0.65934	0.1741	62
			DESC 99	0.41027	0.28399	0.5927	0.1857	62
		Treatment	FIVE 98	0.31464	0.19209	0.51537	0.2558	159
			FIVE 99	0.24472	0.14147	0.42331	0.2852	159
			JOHN 98	0.33212	0.20496	0.53815	0.25	159
			JOHN 99	0.45447	0.29686	0.69577	0.2199	159
			TRUC 98	0.10488	0.047584	0.23116	0.4202	159
			TRUC 99	0.24472	0.14147	0.42331	0.2852	159
	Old Growth	Treatment	KIRK 98	0.15359	0.08072	0.29224	0.3315	75
			KIRK 99	0.20944	0.11831	0.37077	0.2927	75
			MONA 98	0.25133	0.14731	0.42879	0.2731	75
			MONA99	0.15359	0.08072	0.29224	0.3315	75
			NISQ 98	0.2234	0.12791	0.39017	0.2855	75
			NISQ 99	0.027925	0.0077026	0.10124	0.7204	75
			TOPN 98	0.041888	0.014021	0.12514	0.5936	75
			TOPN 99	0.013963	0.0026291	0.074152	1.0095	75
Brown Creeper	Comm Thin	Stand	FIVE 98	0.75223	0.42969	1.3169	0.2837	46
			FIVE 99	1.4104	0.89915	2.2125	0.2265	46
		Treatment	DESC 98	0.094755	0.026054	0.34461	0.7248	87
			DESC 99	0.47377	0.23935	0.93781	0.354	87
			JOHN 98	0.28426	0.12361	0.6537	0.4382	87
			JOHN 99	0.52115	0.26964	1.0073	0.341	87
			TRUC 98	0.33164	0.1515	0.72597	0.4101	87
			TRUC 99	0.37902	0.18018	0.79729	0.3877	87
	Old Growth	Stand	KIRK 98	0.98517	0.52659	1.8431	0.3197	50

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Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			KIRK 99	1.7111	0.98067	2.9855	0.2826	50
			MONA 98	0.57089	0.31186	1.0451	0.3038	33
			MONA99	0.81556	0.47884	1.389	0.2662	33
			TOPN 98	0.45942	0.24528	0.86054	0.3151	31
			TOPN 99	0.63612	0.36382	1.1122	0.2791	31
		Treatment	NISQ 98	0.53411	0.2777	1.0273	0.3432	145
			NISQ 99	0.49851	0.256	0.97074	0.3501	145
Blk-td. G. Warb.	Comm Thin	Stand	DESC98	0.61496	0.38969	0.97047	0.2296	46
			DESC99	0.67087	0.4321	1.0416	0.2212	46
		Treatment	FIVE98	0.12251	0.051126	0.29354	0.4579	56
			FIVE99	0	0	0	0	56
			JOHN98	0	0	0	0	56
			JOHN99	0.12251	0.051126	0.29354	0.4579	56
			TRUC98	0	0	0	0	56
			TRUC99	0	0	0	0	56
	Old Growth	CT&OG	KIRK98	0.098004	0.037437	0.25656	0.5096	56
			KIRK99	0	0	0	0	56
Chst.-bd. Chick.	Clearcut	Treatment	GALL 98	1.2397	0.70843	2.1694	0.2836	47
			GALL 99	1.1511	0.64606	2.0511	0.2931	47
			MINE 98	1.0626	0.5844	1.9321	0.3038	47
			MINE 99	0.1771	0.048723	0.64373	0.7134	47
			OBRI 98	0.5313	0.2365	1.1936	0.4191	47
			OBRI 99	0	0	0	0	47
			TURN 98	0	0	0	0	47
			TURN 99	0	0	0	0	47
	Comm Thin	Stand	JOHN 99	0.94498	0.59535	1.4999	0.2294	31
		Treatment	DESC 98	1.5425	1.0158	2.3424	0.2156	174
			DESC 99	0.9115	0.5328	1.5594	0.2792	174
			FIVE 98	2.1736	1.5247	3.0987	0.1824	174
			FIVE 99	1.823	1.2396	2.6809	0.1987	174
			JOHN 98	0.98162	0.58456	1.6484	0.2692	174
			TRUC 98	2.5242	1.8143	3.5118	0.1697	174
			TRUC 99	1.2621	0.79691	1.9988	0.2378	174

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Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
	Old Growth	Treatment	KIRK 98	1.8238	1.2399	2.6827	0.1988	250
			KIRK 99	1.412	0.91996	2.1671	0.2212	250
			MONA 98	2.7651	1.9903	3.8416	0.1689	250
			MONA99	1.9414	1.3325	2.8288	0.1938	250
			NISQ 98	1.8238	1.2399	2.6827	0.1988	250
			NISQ 99	1.3531	0.87489	2.0928	0.2253	250
			TOPN 98	1.6473	1.1019	2.4626	0.2073	250
			TOPN 99	1.9414	1.3325	2.8288	0.1938	250
Com. Yellowtht.	Clearcut	Treatment	GALL 98	0	0	0	0	178
			GALL 99	0	0	0	0	178
			MINE 98	0	0	0	0	178
			MINE 99	0	0	0	0	178
			OBRI 98	1.7987	1.161	2.7867	0.2262	178
			OBRI 99	2.2893	1.5425	3.3976	0.2035	178
			TURN 98	6.3772	4.89	8.3168	0.1361	178
			TURN 99	4.3332	3.1929	5.8808	0.1568	178
Dark-eyed Jun.	Clearcut	Stand	OBRI 98	1.5243	1.0361	2.2424	0.1952	65
			OBRI 99	1.1535	0.75271	1.7677	0.2163	65
		Treatment	GALL 98	2.2665	1.3836	3.7127	0.2558	206
			GALL 99	2.2665	1.3836	3.7127	0.2558	206
			MINE 98	5.2227	3.5284	7.7307	0.2021	206
			MINE 99	3.5475	2.3033	5.4639	0.2231	206
			TURN 98	0.88688	0.44358	1.7732	0.3648	206
			TURN 99	0.29563	0.10032	0.87116	0.5961	206
	Comm Thin	Treatment	DESC 98	1.101	0.73752	1.6436	0.2066	182
			DESC 99	0.55049	0.3213	0.94318	0.28	182
			FIVE 98	0.078642	0.022415	0.27591	0.712	182
			FIVE 99	0.31457	0.15777	0.62719	0.3633	182
			JOHN 98	2.1233	1.556	2.8976	0.1596	182
			JOHN 99	1.4942	1.0481	2.1302	0.1824	182
			TRUC 98	1.1796	0.79904	1.7415	0.2007	182
			TRUC 99	0.39321	0.21051	0.73446	0.327	182
	Old Growth	Treatment	KIRK 98	0.2684	0.12298	0.58578	0.3981	33

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Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			KIRK 99	0.11503	0.037783	0.35021	0.5907	33
			MONA 98	0.15337	0.057124	0.41179	0.5154	33
			MONA99	0.15337	0.057124	0.41179	0.5154	33
			NISQ 98	0.11503	0.037783	0.35021	0.5907	33
			NISQ 99	0.34509	0.17087	0.69694	0.356	33
			TOPN 98	0.15337	0.057124	0.41179	0.5154	33
			TOPN 99	0.038343	0.0069787	0.21067	1.0078	33
Gold.-crd. King.	Comm Thin	Treatment	DESC 98	2.0581	1.2616	3.3576	0.2529	102
			DESC 99	2.5482	1.6183	4.0124	0.234	102
			FIVE 98	1.9601	1.191	3.2258	0.2575	102
			FIVE 99	0.19601	0.055131	0.6969	0.7186	102
			JOHN 98	0.88205	0.44648	1.7426	0.357	102
			JOHN 99	0.58803	0.26266	1.3165	0.4278	102
			TRUC 98	1.1761	0.64162	2.1557	0.3157	102
			TRUC 99	0.58803	0.26266	1.3165	0.4278	102
	Old Growth	Stand	MONA99	1.5517	0.92173	2.6121	0.2616	38
			NISQ 98	2.436	1.592	3.7274	0.2138	47
			NISQ 99	1.596	0.96744	2.6329	0.2527	47
			TOPN 98	2.3047	1.6123	3.2945	0.181	78
			TOPN 99	2.1923	1.5235	3.1547	0.1844	78
		Treatment	KIRK 98	1.2863	0.70647	2.3421	0.313	191
			KIRK 99	0.51453	0.23518	1.1257	0.4159	191
			MONA 98	1.3506	0.74701	2.4421	0.3092	191
Hm/Town. Warb.	Comm Thin	Treatment	DESC 98	0.83997	0.57547	1.226	0.1948	204
			DESC 99	0.56649	0.36874	0.87029	0.2217	204
			FIVE 98	0.46882	0.29629	0.74181	0.2374	204
			FIVE 99	0.41022	0.25337	0.66415	0.2496	204
			JOHN 98	0.76183	0.51598	1.1248	0.2008	204
			JOHN 99	0.62509	0.41264	0.94693	0.2143	204
			TRUC 98	0.27348	0.1557	0.48035	0.2934	204
			TRUC 99	0.078137	0.030226	0.20199	0.5145	204
	Old Growth	Treatment	KIRK 98	0.38053	0.24372	0.59411	0.2303	113
			KIRK 99	0.33089	0.20652	0.53016	0.244	113

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			MONA 98	0	0	0	0	113
			MONA99	0.1489	0.076842	0.28853	0.3474	113
			NISQ 98	0.39707	0.25623	0.61532	0.2263	113
			NISQ 99	0.38053	0.24372	0.59411	0.2303	113
			TOPN 98	0.18199	0.09924	0.33374	0.3169	113
			TOPN 99	0.049634	0.017123	0.14387	0.5856	113
Hutton's Vireo	Comm Thin	Treatment	DESC 98	0.35503	0.22161	0.56877	0.2374	46
			DESC 99	0.13892	0.069808	0.27647	0.3521	46
			FIVE 98	0.046308	0.015452	0.13878	0.5884	46
			FIVE 99	0.13892	0.069808	0.27647	0.3521	46
			JOHN 98	0.046308	0.015452	0.13878	0.5884	46
			JOHN 99	0.030872	0.0084539	0.11274	0.7161	46
			TRUC 98	0	0.0028663	0.083127	0.0064	46
			TRUC 99	0	0	0	0	46
	Old Growth	CT&OG	KIRK 98	0.013697	0.0025568	0.073374	1.0083	55
			KIRK 99	0.027393	0.0075153	0.09985	0.7188	55
			MONA 98	0	0	0	0	55
			MONA99	0.027393	0.0075153	0.09985	0.7188	55
			NISQ 98	0	0	0	0	55
			NISQ 99	0	0	0	0	55
			TOPN 98	0.013697	0.0025568	0.073374	1.0083	55
			TOPN 99	0.013697	0.0025568	0.073374	1.0083	55
MacGilly's Warb.	Clearcut	Treatment	GALL 98	0.87608	0.59438	1.2913	0.1999	234
			GALL 99	0.35043	0.19714	0.62291	0.2999	234
			MINE 98	1.0221	0.70989	1.4716	0.1876	234
			MINE 99	0.64246	0.41311	0.99914	0.2282	234
			OBRI 98	1.9274	1.4456	2.5697	0.1475	234
			OBRI 99	0.81767	0.5486	1.2187	0.2057	234
			TURN 98	0.73007	0.48047	1.1093	0.2159	234
			TURN 99	0.52565	0.32482	0.85065	0.2493	234
Org.-crnd. Warb.	Clearcut	Treatment	GALL 98	1.0148	0.68982	1.4928	0.1989	259
			GALL 99	1.7664	1.308	2.3856	0.1542	259
			MINE 98	1.1651	0.81097	1.6739	0.1865	259

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			MINE 99	1.0524	0.71995	1.5382	0.1955	259
			OBRI 98	0.56376	0.33959	0.93592	0.263	259
			OBRI 99	0.7141	0.45347	1.1245	0.2348	259
			TURN 98	1.1651	0.81097	1.6739	0.1865	259
			TURN 99	2.255	1.7213	2.9544	0.1385	259
Pacific-slope Fly.	Clearcut	Treatment	GALL 98	0.30461	0.14556	0.63744	0.3742	31
			GALL 99	0.25774	0.1191	0.5578	0.3924	31
			MINE 98	0.046862	0.011987	0.1832	0.7504	31
			MINE 99	0	0	0	0	31
			OBRI 98	0	0	0	0	31
			OBRI 99	0.11716	0.043712	0.314	0.5129	31
			TURN 98	0	0	0	0	31
			TURN 99	0	0	0	0	31
	Comm Thin	Stand	DESC 98	0.38197	0.25966	0.5619	0.1925	38
			DESC 99	0.14147	0.075735	0.26426	0.3162	38
		Treatment	FIVE 98	2.2103	1.6717	2.9225	0.1432	272
			FIVE 99	0.88951	0.60736	1.3027	0.1965	272
			JOHN 98	1.3477	0.97131	1.8701	0.1683	272
			JOHN 99	0.48519	0.29792	0.79017	0.2527	272
			TRUC 98	0.91646	0.62849	1.3364	0.1942	272
			TRUC 99	0.5391	0.33807	0.85966	0.2415	272
	Old Growth	Stand	MONA 98	1.5254	1.0671	2.1806	0.1804	63
			MONA99	1.2288	0.83049	1.8182	0.1981	63
		Treatment	KIRK 98	1.571	1.1525	2.1416	0.1591	247
			KIRK 99	0.96467	0.66616	1.397	0.1906	247
			NISQ 98	1.1852	0.84143	1.6693	0.1761	247
			NISQ 99	0.7993	0.5365	1.1908	0.2055	247
			TOPN 98	0.27562	0.14723	0.51597	0.3283	247
			TOPN 99	0.38587	0.22462	0.66287	0.2814	247
Red-brsd. Nut.	Comm Thin	Treatment	DESC 98	0.01441	0.0025779	0.080548	1.0171	30
			DESC 99	0	0	0	0	30
			FIVE 98	0.12969	0.061078	0.27537	0.3816	30
			FIVE 99	0.028819	0.0075745	0.10965	0.7311	30

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
	Old Growth	Treatment	JOHN 98	0.028819	0.0075745	0.10965	0.7311	30
			JOHN 99	0.057639	0.020747	0.16013	0.5334	30
			TRUC 98	0.12969	0.061078	0.27537	0.3816	30
			TRUC 99	0.057639	0.020747	0.16013	0.5334	30
			KIRK 98	0.15088	0.079427	0.28662	0.3308	77
			KIRK 99	0.10973	0.052924	0.22752	0.3789	77
			MONA 98	0.13717	0.070442	0.26709	0.3443	77
			MONA99	0.35663	0.22316	0.56992	0.2388	77
			NISQ 98	0	0	0	0	77
			NISQ 99	0.054866	0.020777	0.14489	0.5182	77
			TOPN 98	0.12345	0.061599	0.2474	0.3601	77
			TOPN 99	0.12345	0.061599	0.2474	0.3601	77
Song Sparrow	Clearcut	Treatment	GALL 98	1.2267	0.80988	1.8582	0.2143	403
			GALL 99	0.92006	0.5737	1.4755	0.2445	403
			MINE 98	1.8401	1.2994	2.6059	0.1789	403
			MINE 99	1.1756	0.77001	1.7949	0.2184	403
			OBRI 98	3.6802	2.83	4.7859	0.1346	403
			OBRI 99	2.9646	2.2278	3.9451	0.1466	403
			TURN 98	4.2936	3.3505	5.5023	0.1271	403
			TURN 99	4.6003	3.6119	5.8593	0.1239	403
Spotted Towhee	Clearcut	Treatment	GALL 98	0.71867	0.45306	1.14	0.2387	235
			GALL 99	0.34042	0.17809	0.6507	0.3398	235
			MINE 98	1.0591	0.71819	1.5618	0.2001	235
			MINE 99	0.94561	0.62865	1.4224	0.2106	235
			OBRI 98	1.1726	0.80863	1.7003	0.1913	235
			OBRI 99	1.1726	0.80863	1.7003	0.1913	235
			TURN 98	2.2695	1.7108	3.0107	0.1449	235
			TURN 99	1.4373	1.0224	2.0206	0.1751	235
Swain. Thrush	Clearcut	Treatment	GALL 98	0.53631	0.33224	0.86574	0.248	140
			GALL 99	0.56611	0.35464	0.90366	0.242	140
			MINE 98	0.35754	0.20155	0.63425	0.2988	140
			MINE 99	1.3408	0.96708	1.8589	0.1679	140
			OBRI 98	0.23836	0.11985	0.47407	0.3619	140

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			OBRI 99	0.41713	0.24428	0.7123	0.2782	140
			TURN 98	0.32775	0.1806	0.59479	0.3112	140
			TURN 99	0.44693	0.26598	0.75096	0.2695	140
	Comm Thin	Treatment	DESC 98	0.34235	0.18271	0.64148	0.3212	55
			DESC 99	0.22823	0.113	0.46098	0.3619	55
			FIVE 98	0.13314	0.057662	0.3074	0.4364	55
			FIVE 99	0.13314	0.057662	0.3074	0.4364	55
			JOHN 98	0.038039	0.010118	0.14301	0.74	55
			JOHN 99	0.076077	0.027354	0.21159	0.5455	55
			TRUC 98	0.11412	0.047191	0.27595	0.4629	55
			TRUC 99	0.057058	0.018275	0.17814	0.6172	55
	Old Growth	Treatment	KIRK 98	0.025167	0.004391	0.14424	1.0224	24
			KIRK 99	0.2265	0.10311	0.49757	0.3956	24
			MONA 98	0.075501	0.023441	0.24318	0.6154	24
			MONA99	0.12584	0.047853	0.3309	0.4953	24
			NISQ 98	0	0	0	0	24
			NISQ 99	0.050334	0.012897	0.19645	0.7385	24
			TOPN 98	0	0	0	0	24
			TOPN 99	0.12584	0.047853	0.3309	0.4953	24
Varied Thrush	Clearcut	Treatment	GALL 98	0.024868	0.0068667	0.09006	0.7071	40
			GALL 99	0.13677	0.075353	0.24826	0.3015	40
			MINE 98	0.11191	0.05807	0.21565	0.3333	40
			MINE 99	0.18651	0.11162	0.31166	0.2582	40
			OBRI 98	0	0	0	0	40
			OBRI 99	0	0	0	0	40
			TURN 98	0	0	0	0	40
			TURN 99	0.012434	0.0023114	0.066888	1	40
	Comm Thin	Stand	TRUC 98	0.1499	0.092305	0.24342	0.2425	36
			TRUC 99	0.16753	0.10583	0.2652	0.2294	36
		Treatment	DESC 98	0	0	0	0	67
			DESC 99	0.17544	0.0879	0.35017	0.3571	67
			FIVE 98	0.15949	0.078112	0.32566	0.3696	67
			FIVE 99	0.19139	0.097798	0.37456	0.3463	67

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			JOHN 98	0	0	0	0	67
			JOHN 99	0	0	0	0	67
	Old Growth	Treatment	KIRK 98	0.20527	0.1345	0.31327	0.2182	168
			KIRK 99	0.19549	0.1268	0.30141	0.2236	168
			MONA 98	0.10752	0.060312	0.19168	0.3015	168
			MONA99	0.27369	0.18958	0.39511	0.189	168
			NISQ 98	0.25414	0.17366	0.37191	0.1961	168
			NISQ 99	0.16617	0.104	0.2655	0.2425	168
			TOPN 98	0.21504	0.14225	0.32508	0.2132	168
			TOPN 99	0.29324	0.20563	0.41818	0.1826	168
White-crd. Sp.	Clearcut	Treatment	GALL 98	0.01668	0.0031142	0.089339	1.0131	64
			GALL 99	0.03336	0.009104	0.12224	0.7255	64
			MINE 98	0.11676	0.053013	0.25716	0.4113	64
			MINE 99	0.10008	0.043251	0.23158	0.4393	64
			OBRI 98	0.21684	0.11594	0.40554	0.3214	64
			OBRI 99	0.18348	0.094361	0.35676	0.3424	64
			TURN 98	0.28356	0.16021	0.50188	0.2918	64
			TURN 99	0.13344	0.063051	0.28241	0.389	64
Willow Fly.	Clearcut	Stand	MINE 98	1.5333	1.0979	2.1414	0.1696	97
			MINE 99	1.4131	1.0023	1.9921	0.1744	97
			OBRI 98	2.5477	1.7584	3.6913	0.1909	118
			OBRI 99	2.7673	1.9233	3.9819	0.1873	118
		Treatment	GALL 98	1.1781	0.73514	1.888	0.2441	363
			GALL 99	0.41803	0.21709	0.80498	0.3439	363
			TURN 98	2.2042	1.4638	3.3191	0.2112	363
			TURN 99	1.7481	1.1383	2.6848	0.2215	363
Wilson's Warb.	Clearcut	Stand	GALL 98	0.33903	0.2357	0.21073	0.54544	29
			GALL 99	0.18835	0.3162	0.10018	0.35412	29
			OBRI 98	0.3197	0.2132	0.20786	0.49173	30
			OBRI 99	0.13079	0.3333	0.067408	0.25376	30
		Treatment	MINE 98	0.8306	0.1941	0.56981	1.2107	122
			MINE 99	0.24693	0.3187	0.13424	0.45425	122
			TURN 98	0.13469	0.4211	0.061016	0.29733	122

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
			TURN 99	0.22449	0.3326	0.11898	0.42357	122
	Comm Thin	Stand	FIVE 98	0.1624	0.3162	0.08545	0.30866	21
			FIVE 99	0.1624	0.3162	0.08545	0.30866	21
			JOHN 98	0	0	0	0	21
			JOHN 99	0	0	0	0	21
			TRUC 98	0.099472	0.3536	0.04709	0.21012	12
			TRUC 99	0.06217	0.4472	0.024519	0.15764	12
		Treatment	DESC 98	0.53606	0.2713	0.31439	0.914	57
			DESC 99	0.26803	0.3689	0.13109	0.54801	57
	Old Growth	Stand	KIRK 98	0.18415	0.378	0.082388	0.41159	11
			KIRK 99	0.13153	0.4472	0.05139	0.33666	11
			MONA 98	0.063662	0.7071	0.014661	0.27643	8
			MONA99	0.19099	0.4082	0.077232	0.47228	8
			TOPN 99	0	0	0	0	1
		Treatment	NISQ 98	0.27633	0.395	0.12732	0.59974	33
			NISQ 99	0.27633	0.395	0.12732	0.59974	33
			TOPN 98	0.039475	1.0066	0.0071952	0.21657	33
Winter Wren	Clearcut	Treatment	GALL 98	1.2543	0.88479	1.778	0.1795	111
			GALL 99	1.4036	1.0039	1.9625	0.1723	111
			MINE 98	0.44795	0.26438	0.759	0.274	111
			MINE 99	0.20905	0.10018	0.43622	0.3889	111
			OBRI 98	0.029864	0.0058119	0.15345	1.0042	111
			OBRI 99	0.029864	0.0058119	0.15345	1.0042	111
			TURN 98	0	0	0	0	111
			TURN 99	0	0	0	0	111
	Comm Thin	Stand	DESC 99	5.7278	4.6343	7.0793	0.1084	121
			JOHN 99	2.8226	2.1589	3.6904	0.1356	88
			TRUC 98	6.489	1.0645	39.555	1.1281	69
		Treatment	DESC 98	2.3787	1.7176	3.2941	0.1673	696
			FIVE 98	3.6644	2.7226	4.932	0.1524	696
			FIVE 99	3.9216	2.9243	5.2589	0.1505	696
			JOHN 98	2.3144	1.6676	3.212	0.1684	696
			TRUC 99	1.2215	0.82546	1.8075	0.202	696

Appendix 1. Summary of output from program DISTANCE, listing density estimates and associated statistics for 21 bird species.

Bird Species	Forest Treatment	Detection Function	Stand & Year	Bird Density (No. / Ha)	Lower Confidence Limit	Upper Confidence Limit	Coefficent of Variation	Degrees of Freedom
	Old Growth	Stand Treatment	KIRK 99	1.0186	0.80602	1.2872	0.1179	72
			KIRK 98	1.7452	1.3309	2.2887	0.139	565
			MONA 98	2.2058	1.7177	2.8325	0.1281	565
			MONA99	1.9149	1.473	2.4894	0.1345	565
			NISQ 98	2.0604	1.5952	2.6611	0.1311	565
			NISQ 99	1.3574	1.0083	1.8274	0.1526	565
			TOPN 98	1.7695	1.3511	2.3174	0.1383	565
			TOPN 99	1.0665	0.76939	1.4784	0.1678	565

Appendix 2. Summary of guild assignments[a] for 26 species of forest birds included in correlation analyses of abundance, density, and reproduction in the southwest Cascade Mountains of Washington, 1998–1999.

Bird Species	Migratory Guild	Nesting Guild	Feeding Guild
American Robin	Permanent Resident	Open-cup Nesting	Ground Feeding
Black-headed Grosbeak	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Brown Creeper	Permanent Resident	Cavity Nesting	Bark Gleaning
Chestnut-backed Chickadee	Permanent Resident	Cavity Nesting	Foliage Gleaning
Chipping Sparrow	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Dark-eyed Junco	Permanent Resident	Ground Nesting	Ground Feeding
Dusky Flycatcher	Migratory (Neotropical or short-distance)	Open-cup Nesting	Aerial Feeding
Hairy Woodpecker	Permanent Resident	Cavity Nesting	Bark Gleaning
House Wren	Migratory (Neotropical or short-distance)	Cavity Nesting	Foliage Gleaning
MacGillivray's Warbler	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Mountain Chickadee	Permanent Resident	Cavity Nesting	Foliage Gleaning
Northern Flicker	Permanent Resident	Cavity Nesting	Bark Gleaning
Orange-crowned Warbler	Migratory (Neotropical or short-distance)	Ground Nesting	Foliage Gleaning
Pacific-slope Flycatcher	Migratory (Neotropical or short-distance)	Open-cup Nesting	Aerial Feeding
Red-breasted Nuthatch	Permanent Resident	Cavity Nesting	Bark Gleaning
Rufous Hummingbird	Migratory (Neotropical or short-distance)	Open-cup Nesting	Aerial Feeding
Song Sparrow	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Spotted Towhee	Permanent Resident	Open-cup Nesting	Foliage Gleaning
Swainson's Thrush	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Townsend's Solitaire	Permanent Resident	Ground Nesting	Ground Feeding
Varied Thrush	Permanent Resident	Open-cup Nesting	Foliage Gleaning
Warbling Vireo	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Western Tanager	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Willow Flycatcher	Migratory (Neotropical or short-distance)	Open-cup Nesting	Aerial Feeding
Wilson's Warbler	Migratory (Neotropical or short-distance)	Open-cup Nesting	Foliage Gleaning
Winter Wren	Permanent Resident	Cavity Nesting	Foliage Gleaning

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[a] Guild assignments followed those of Erhlich et al. (1988) and Sallabanks et al. (2001a).

Appendix 3. List of plant species recorded during plot- and nest-level habitat sampling in the southwest Cascade Mountains of Washington, 1998–1999.

Field Code	Scientific Name	Common Name
Trees		
ABIAMA	*Abies amabilis*	Pacific Silver Fir
ABIGRA	*Abies grandis*	Grand Fir
ABIPRO	*Abies procera*	Noble Fir
ACEMAC	*Acer macrophyllum*	Bigleaf Maple
ALNRUB	*Alnus rubra*	Red Alder
BETPAP	*Betula papyrifera*	Paper Birch
FRALAT	*Fraxinus latifolia*	Oregon Ash
POPBAL	*Populus balsamifera*	Black Cottonwood
PRUEMA	*Prunus emarginata*	Bitter Cherry
PRUSPP	*Prunus* species	
PSEMEN	*Pseudotsuga menziesii*	Douglas-fir
ROOTBALL		
SALLUC	*Salix lucida*	Pacific Willow
SALSCO	*Salix scouleriana*	Scouler's Willow
SALSPP	*Salix* species	
TAXBRE	*Taxus brevifolia*	Western Yew
THUPLI	*Thuja plicata*	Western Red Cedar
TSUHET	*Tsuga heterophylla*	Western Hemlock
TSUMER	*Tsuga mertensiana*	Mountain Hemlock
UNK STUMP		
UNK SNAG		
Shrubs		
ACECIR	*Acer circinatum*	Vine Maple
AMEALN	*Amelanchier alnifolia*	Saskatoon/Serviceberry
ARUSYL	*Aruncus sylvester*	Goatsbeard
BERNER	*Berberis nervosa*	Oregon Grape
CORCOR	*Corylus cornuta*	California Hazelnut
CORSTO	*Cornus stolonifera*	Red-osier Dogwood

Appendix 3. List of plant species recorded during plot- and nest-level habitat sampling in the southwest Cascade Mountains of Washington, 1998–1999.

CYTSCO	*Cytisus scoparius*	Scotch Broom
GAUSHA	*Gaultheria shallon*	Salal
HOLDIS	*Holdiscus discolor*	Oceanspray
OEMCER	*Oemleria cerasiformis*	Indian Plum/Osoberry
OPLHOR	*Oplopanax horridus*	Devil's Club
PHYCAP	*Physocarpus capitatus*	Pacific Ninebark
RHAPUR	*Rhamnus purshiana*	Cascara
RIBDIV	*Ribes divaricatum*	Wild Gooseberry
RIBLAC	*Ribes lacustre*	Black Gooseberry
RIBSAN	*Ribes sanguineum*	Red-flowering Currant
ROSGYM	*Rosa gymnocarpa*	Baldhip Rose
ROSNUT	*Rosa nutkana*	Nootka Rose
ROSSPP	*Rosa* species	
RUBDIS	*Rubus discolor*	Himalayan Blackberry
RUBLAC	*Rubus laciniatus*	Evergreen Blackberry
RUBLEU	*Rubus leucodermis*	Black Raspberry
RUBPAR	*Rubus parviflorus*	Thimbleberry
RUBSPP	*Rubus* species	
RUBSPE	*Rubus spectabilis*	Salmonberry
RUBURS	*Rubus ursinus*	Trailing Blackberry
SAMRAC	*Sambucus racemosa*	Red Elderberry
SORSIT	*Sorbus sitchensis*	Sitka Mountain-Ash
SPIDOU	*Spirea douglasii*	Hardhack/Douglas Spirea
SYMALB	*Symphoricarpos albus*	Common Snowberry
UNK SHRUB		
VACOVA	*Vaccinium ovatum*	Evergreen Huckleberry
VACPAR	*Vaccinium parvifolium*	Red Huckleberry
VACSPP	*Vaccinium* species	
VIBEDU	*Viburnum edule*	High-bush Cranberry

Other/Forbs

ANAMAR	*Anaphalis margaritacea*	Pearly Everlasting
ASTSPP	*Aster* species	

Appendix 3. List of plant species recorded during plot- and nest-level habitat sampling in the southwest Cascade Mountains of Washington, 1998–1999.

ATHFIL	*Athyrium felix-femina*	Lady Fern
BLESPI	*Blechnum spicant*	Deer Fern
CARAQU	*Carex aquatilis*	Water Sedge
CARSPP	*Carex* species	
CIRARV	*Cirsium arvense*	Canada Thistle
CIRSPP	*Cirsium species*	Thistles
CRECAP	*Crepis capillaris*	Smooth Hawksbeard
DAUCAR	*Daucus carota*	Wild Carrot, Queen Anne's Lace
DIGPUR	*Digitalis purpureus*	Foxglove
DISHOO	*Disporum hookeri*	Hooker's Fairybell
EPIANG	*Epilobium angustifolium*	Fireweed
EQUARV	*Equisetum arvense*	Common Horsetail
EQUSPP	*Equisetum* species	
GALSPP	*Galium* species	
JUNSPP	*Juncus* species	
LACMUR	*Lactuca muralis*	Wall Lettuce
PETPAL	*Petasites palmatus*	Colts Foot
POLMUN	*Polystichum munitum*	Sword Fern
PTEAQU	*Pteridium aquilinum*	Bracken Fern
SCIMIC	*Scirpus microcarpus*	Small-flowered Bulrush
SOLCAN	*Solidago canadensis*	Canada Goldenrod
SOLDUL	*Solanum dulcamara*	European Bittersweet
STACOO	*Stachys cooleyae*	Cooley's Hedge-nettle
TRIOVA	*Trillium ovatum*	Western Trillium
TYPLAT	*Typha latifolia*	Cattail
UNK FORB		
UNK GRASS		
UNK SEDGE		
URTDIO	*Urtica dioica*	Stinging Nettle
VERBEC	*Veronica beccabunga*	American Brooklime
VICSPP	*Vicia* species	Vetches

Appendix 4. Mean values of ground cover (%) calculated from ocular estimates for all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999.

Forest Treatment	Plot Name	BLESHRB	BPDSHRB	BRNCHS	BRSOIL	CWDEBR	FERN	FORBS	FWDEBR	GRASS
Clearcut	Gallup	5.94	17.19	0.00	1.33	12.73	4.30	17.03	7.58	4.92
Clearcut	Mineral	3.28	10.70	0.00	1.09	19.06	2.19	10.16	12.11	0.78
Clearcut	O'Brian	1.09	13.05	4.45	0.94	4.14	18.44	27.27	3.67	3.91
Clearcut	Turner	3.52	30.83	4.06	0.00	0.16	19.66	16.38	1.80	5.63
Commercial Thin	Deschutes	24.14	18.52	0.00	0.16	0.78	12.03	11.41	10.86	1.33
Commercial Thin	Five-O-One	6.72	10.31	1.33	0.78	2.66	32.81	6.25	8.28	0.55
Commercial Thin	Johnson	2.42	5.00	0.00	0.86	6.33	14.30	29.38	14.38	6.56
Commercial Thin	Truck	6.72	8.67	0.00	0.00	3.67	17.19	12.66	11.56	2.89
Old Growth	Kirkland Pass	13.98	0.63	0.31	0.70	5.08	15.00	1.33	18.59	0.00
Old Growth	Mona	8.13	1.48	0.00	0.78	8.20	10.00	7.20	16.25	0.00
Old Growth	Nisqually	9.53	2.89	0.00	0.08	11.56	6.64	6.25	16.80	0.00
Old Growth	Top Notch	1.25	4.30	0.00	0.00	16.64	5.08	3.98	20.86	0.00

Forest Treatment	Plot Name	LFLTTR	LOBARIA	MOSS	ODSHRB	OTHER	ROCK	STUMP	TRESEED
Clearcut	Gallup	11.02	0.00	7.50	3.59	0.39	0.70	2.19	5.16
Clearcut	Mineral	5.78	0.16	3.28	0.39	6.64	6.02	3.83	13.75
Clearcut	O'Brian	7.66	0.23	0.94	3.05	0.08	0.23	2.11	2.81
Clearcut	Turner	2.81	0.08	0.08	1.56	7.81	0.00	0.63	3.36
Commercial Thin	Deschutes	11.88	0.00	4.77	0.94	1.09	0.16	1.56	0.16
Commercial Thin	Five-O-One	10.78	0.00	9.53	0.16	3.75	0.00	1.09	3.83
Commercial Thin	Johnson	8.05	0.16	3.28	4.38	2.73	0.00	1.17	0.23
Commercial Thin	Truck	11.88	0.00	7.34	2.81	1.17	1.72	2.81	9.61
Old Growth	Kirkland Pass	36.25	0.47	3.20	0.39	3.13	0.47	0.00	0.08
Old Growth	Mona	28.67	0.00	6.64	1.56	5.08	2.03	3.28	0.70
Old Growth	Nisqually	23.52	0.00	6.48	0.47	9.69	0.00	0.00	6.48
Old Growth	Top Notch	29.45	0.31	2.97	0.31	1.33	0.70	2.81	13.36

Cover type definitions as follows: broad-leaved evergreen shrubs < 1m tall (BLESHRB), berry-producing deciduous shrubs < 1m tall (BPDSHRB), branches (BRNCHS), bare soil (BRSOIL), coarse woody debris (CWDEBR), ferns (FERN), forbs (FORBS), fine woody debris (FWDEBR), grass (GRASS), leaf litter (LFLTTR), *Lobaria* lichen (LOBARIA), moss (MOSS), other deciduous shrubs < 1m tall (ODSHRB), other (e.g., saprophytes, above-ground roots, tree and snag boles; OTHER), rock (ROCK), stumps (STUMP), tree seedlings < 1m tall (TRESEED).

Appendix 5. Mean diameter-at-breast-height (DBH) and density of tree species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Forest Treatment	Plot Name	Tree Species	Mean DBH (cm)	Density (Ha^{-1})
Clearcut	Gallup	ALNRUB	11.11	92.19
		ALNRUB SNAG	4.00	9.38
		FRALAT	4.00	1.56
		POPBAL	0.50	1.56
		PRUSPP	0.50	4.69
		PSEMEN	11.68	114.06
		PSEMEN SNAG	12.00	1.56
		SALSPP	1.00	12.50
		THUPLI	1.42	9.38
		TSUHET	4.88	100.00
		UNK SNAG	42.57	10.94
		UNK STUMP	61.54	118.75
	Mineral	ABIAMA	3.00	15.63
		ABIPRO	5.14	10.94
		POPBAL	0.50	6.25
		PSEMEN	6.40	146.88
		SALSPP	0.50	9.38
		THUPLI	0.80	7.81
		TSUHET	3.49	259.38
		TSUMER	2.20	165.63
		UNK SNAG	3.33	4.69
		UNK STUMP	61.06	100.00
	O'Brian	ALNRUB	1.00	18.95
		ALNRUB SNAG	4.00	18.95
		POPBAL	0.76	322.08
		PRUEMA	0.80	123.13
		PRUSPP	0.67	111.30
		PSEMEN	8.66	380.18
		PSEMEN STUMP	71.11	186.35
		SALSPP	1.00	171.67
		TSUHET	7.09	352.54
		TSUHET STUMP	44.15	82.74
		UNK SNAG	87.00	1.94
		UNK STUMP	48.52	58.05
	Turner	ALNRUB	2.93	1168.29
		ALNRUB STUMP	7.25	37.90
		POPBAL	1.11	346.30
		PRUEMA	0.96	279.41
		PRUSPP	1.75	419.17
		PSEMEN	7.21	517.22
		PSEMEN STUMP	54.55	61.46
		SALSPP	1.20	184.71
		TSUHET	7.25	18.95
		UNK STUMP	79.11	72.54

Appendix 5. Mean diameter-at-breast-height (DBH) and density of tree species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Commercial Thin	Deschutes	ABIGRA	42.13	26.80
		ABIGRA SNAG	9.00	49.72
		ACEMAC	11.48	67.29
		ALNRUB	9.63	50.69
		POPBAL	7.50	9.47
		PSEMEN	36.51	240.04
		PSEMEN SNAG	22.38	10.44
		PSEMEN STUMP	82.85	107.57
		THUPLI	20.83	20.02
		THUPLI STUMP	43.25	6.67
		TSUHET	36.20	42.12
		TSUHET SNAG	3.00	9.47
		TSUHET STUMP	16.67	24.18
		UNK SNAG	7.50	5.71
		UNK STUMP	28.76	42.70
	Five-O-One	ALNRUB	30.89	53.12
		ALNRUB SNAG	18.55	9.58
		ALNRUB STUMP	37.00	49.72
		POPBAL	60.75	25.83
		PSEMEN	53.00	183.12
		PSEMEN SNAG	59.00	1.94
		PSEMEN STUMP	86.81	59.27
		ROOTBALL	362.00	1.94
		THUPLI	42.40	33.73
		THUPLI SNAG	12.00	9.47
		THUPLI STUMP	43.00	7.75
		TSUHET	13.57	1053.22
		TSUHET SNAG	22.95	35.10
		TSUHET STUMP	33.97	33.48
		UNK SNAG	10.00	9.47
		UNK STUMP	62.91	79.65
	Johnson	ABIGRA	43.50	12.50
		ALNRUB	18.69	25.00
		POPBAL	54.23	20.31
		PSEMEN	38.43	182.81
		THUPLI	20.00	6.25
		TSUHET	20.28	14.06
		TSUHET SNAG	24.00	1.56
		UNK SNAG	17.21	21.88
		UNK STUMP	48.67	190.63
	Truck	ABIAMA	25.00	1.56
		ABIGRA	44.00	1.56
		ALNRUB	1.86	592.19
		ALNRUB SNAG	26.00	3.13
		PSEMEN	60.96	79.69
		SALSPP	0.50	3.13
		THUPLI	18.92	20.31
		TSUHET	30.19	137.50
		TSUHET SNAG	18.00	1.56
		UNK SNAG	27.58	20.31
		UNK STUMP	49.22	78.13

Appendix 5. Mean diameter-at-breast-height (DBH) and density of tree species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Old Growth	Kirkland Pass	ACEMAC	45.00	49.72
		PSEMEN	76.32	271.39
		PSEMEN ROOTBALL	333.00	1.94
		PSEMEN SNAG	31.29	71.39
		PSEMEN STUMP	39.60	85.96
		ROOTBALL	800.00	9.47
		THUPLI	29.99	86.40
		THUPLI SNAG	21.75	10.44
		TSUHET	21.57	252.44
		TSUHET SNAG	17.89	27.99
		TSUHET STUMP	27.88	26.80
		UNK DEAD SAPLING	1.00	149.16
		UNK SNAG	10.00	9.47
		UNK STUMP	32.92	11.63
	Mona	ACEMAC	29.25	10.44
		DEAD SAPLING	1.00	49.72
		PSEMEN	86.20	75.99
		PSEMEN ROOTBALL	47.00	49.72
		PSEMEN SNAG	52.00	11.63
		PSEMEN STUMP	80.02	30.07
		ROOTBALL	351.88	8.61
		TAXBRE	20.00	1.94
		THUPLI	31.31	65.15
		THUPLI SNAG	68.85	29.70
		THUPLI STUMP	95.00	1.94
		TSUHET	16.44	1296.33
		TSUHET SNAG	11.32	76.65
		TSUHET STUMP	32.17	7.64
		UNK SNAG	12.00	8.61
		UNK STUMP	63.71	27.67
	Nisqually	ALNRUB	6.95	17.19
		PSEMEN	66.31	164.06
		PSEMEN SNAG	35.67	9.38
		THUPLI	22.24	26.56
		TSUHET	11.31	526.56
		TSUHET SNAG	52.50	3.13
		UNK SNAG	47.65	159.38
		UNK STUMP	102.40	7.81
	Top Notch	ABIAMA	26.55	96.88
		ABIAMA SNAG	20.40	23.44
		ALNRUB	14.77	48.44
		ALNRUB SNAG	4.00	4.69
		PSEMEN	93.00	3.13
		PSEMEN SNAG	101.40	15.63
		THUPLI	42.68	34.38
		TSUHET	32.53	381.25
		TSUHET SNAG	19.00	6.25
		UNK SNAG	37.47	242.19
		UNK STUMP	42.60	46.88

Appendix 6. Stem densities of forb species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Forest Treatment	Plot Name	Forb Species	Density (Ha^{-1})
Clearcut	Gallup	ANAMAR	39.79
		ATHFIL	214.85
		CIRARV	119.36
		DIGPUR	262.60
		EPIANG	5458.85
		EQUARV	39.79
		LACMUR	47.75
		POLMUN	23.87
		PTEAQU	159.15
		UNK FORB	39.79
		UNK GRASS	4082.20
	Mineral	ANAMAR	55.70
		CIRARV	23.87
		EPIANG	6803.66
		EQUARV	31.83
		UNK GRASS	127.32
	O'Brian	ANAMAR	7309.02
		ASTSPP	3281.60
		ATHFIL	497.21
		BLESPI	1044.15
		CIRARV	2088.29
		DIGPUR	944.70
		EPIANG	26053.94
		EQUSPP	596.66
		PETPAL	149.16
		POLMUN	6960.98
		PTEAQU	11833.66
		UNK GRASS	21976.79
	Turner	ANAMAR	696.10
		ATHFIL	1939.13
		CIRARV	5270.45
		CIRSPP	248.61
		EPIANG	8850.38
		POLMUN	42511.67
		PTEAQU	994.43
		VICSPP	99.44

Appendix 6. Stem densities of forb species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Commercial Thin	Deschutes	CIRSPP	99.44
		DIGPUR	49.72
		LACMUR	646.38
		POLMUN	12529.76
		PTEAQU	894.98
		SYMALB	646.38
		UNK FORB	696.10
	Five-O-One	ATHFIL	3231.88
		POLMUN	44699.40
		PTEAQU	447.49
		TRIOVA	99.44
	Johnson	ASTSPP	15.92
		CIRARV	620.69
		CRECAP	7.96
		EPIANG	71.62
		LACMUR	1790.44
		POLMUN	10201.52
		PTEAQU	103.45
		UNK FORB	198.94
		UNK GRASS	143.24
		VERBEC	7.96
	Truck	ATHFIL	326.26
		CIRSPP	23.87
		EPIANG	55.70
		LACMUR	238.73
		POLMUN	4432.33
		PTEAQU	1265.24
		UNK GRASS	159.15
		UNK STUMP	7.96
Old Growth	Kirkland Pass	ATHFIL	99.44
		POLMUN	9496.76
		PTEAQU	99.44
	Mona	POLMUN	5369.90
		PTEAQU	596.66
	Nisqually	EPIANG	87.53
		LACMUR	55.70
		POLMUN	978.77
	Top Notch	ATHFIL	143.24
		POLMUN	350.13
		PTEAQU	103.45

Appendix 7. Stem densities of shrub species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

Forest Treatment	Plot Name	Shrub Species	Density (Ha^{-1})
Clearcut	Gallup	ACECIR	1965.50
		CYTSCO	55.70
		OEMCER	23.87
		OPLHOR	509.28
		RUBLAC	23.87
		RUBSPE	485.41
		RUBURS	254.64
		SAMRAC	23.87
		VACOVA	39.79
		VACPAR	1201.58
		VACSPP	652.52
	Mineral	ACECIR	7.96
		OEMCER	7.96
		RUBURS	79.58
		SORSIT	7.96
		VACPAR	2745.34
		VACSPP	278.51
	O'Brian	ACECIR	1596.04
		BERNER	58.02
		GAUSHA	99.44
		OPLHOR	241.55
		RIBSAN	248.61
		RUBLEU	296.01
		RUBPAR	1159.17
		RUBSPE	2849.79
		RUBURS	499.60
		SAMRAC	355.20
		VACPAR	1115.45
	Turner	ACECIR	739.94
		BERNER	3033.00
		OPLHOR	47.37
		RIBLAC	142.11
		RIBSAN	847.71
		ROSSPP	653.56
		RUBDIS	961.49
		RUBLAC	1989.20
		RUBLEU	323.25
		RUBPAR	2167.87

Appendix 7. Stem densities of shrub species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

		RUBSPE	2461.62
		RUBSPP	66.32
		RUBURS	3527.19
		SAMRAC	676.10
		UNK SHRUB	9.47
		VACPAR	3997.19
Commercial Thin	Deschutes	ACECIR	312.63
		BERNER	434.52
		CORCOR	58.02
		CYTSCO	133.78
		GAUSHA	2241.14
		HOLDIS	1134.21
		ROSSPP	179.97
		RUBLEU	1073.78
		RUBPAR	56.84
		RUBSPE	85.26
		RUBURS	403.72
		SAMRAC	884.52
		SYMALB	18.95
		UNK SHRUB	104.18
		VACPAR	425.05
	Five-O-One	ACECIR	63.93
		GAUSHA	2088.29
		OPLHOR	189.48
		RIBSAN	104.21
		ROSSPP	9.47
		RUBLEU	9.47
		RUBPAR	49.72
		RUBSPE	2199.75
		SAMRAC	600.25
		VACPAR	705.67
		VACSPP	99.44
	Johnson	ACECIR	724.13
		RUBDIS	15.92
		RUBLEU	47.75
		RUBURS	318.30
		SAMRAC	47.75
	Truck	ACECIR	159.15
		OPLHOR	55.70

Appendix 7. Stem densities of shrub species recorded on all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999. Species' codes are defined in Appendix 3.

		RUBLEU	7.96
		RUBSPE	87.53
		RUBURS	175.07
		SAMRAC	95.49
		VACPAR	167.11
Old Growth	Kirkland Pass	ACECIR	9.47
		BERNER	696.10
		GAUSHA	1140.06
		HOLDIS	104.21
		ROSSPP	99.44
		VACPAR	582.54
	Mona	ACECIR	333.87
		BERNER	248.61
		GAUSHA	474.77
		OPLHOR	73.41
		RIBSAN	248.61
		ROSSPP	108.92
		RUBSPE	75.79
		VACPAR	284.15
	Nisqually	ACECIR	103.45
		GAUSHA	183.02
		OEMCER	15.92
		OPLHOR	55.70
		RUBPAR	55.70
		RUBSPE	63.66
		RUBURS	47.75
		SAMRAC	7.96
		VACPAR	564.98
	Top Notch	OEMCER	7.96
		OPLHOR	95.49
		RUBSPE	95.49
		SAMRAC	23.87
		VACPAR	111.41

Appendix 8. Mean values of canopy cover and canopy height for all 12 study plots in the southwest Cascade Mountains of Washington, 1998–1999.

Forest Treatment	Plot Name	Mean Canopy Cover (%)	Mean Canopy Height (m)
Clearcut	Gallup	20.64	7.86
Clearcut	Mineral	26.43	4.86
Clearcut	O'Brian	0.00	0.00
Clearcut	Turner	0.38	0.00
Commercial Thin	Deschutes	85.27	10.67
Commercial Thin	Five-O-One	89.80	16.53
Commercial Thin	Johnson	63.00	35.56
Commercial Thin	Truck	65.63	35.20
Old Growth	Kirkland Pass	84.63	22.30
Old Growth	Mona	92.56	12.72
Old Growth	Nisqually	87.93	62.50
Old Growth	Top Notch	93.31	34.06