

# Does Competition for Roosts Influence Bat Distribution in a Managed Forest?

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## ABSTRACT

Previous studies disagree regarding the mechanism that determines distributions of nearctic bat species. Many papers suggest that competition for foraging areas is important and is dictated by morphological characters or roost diversity. Here, I present evidence that suggests that local bat distribution, diversity, and population size in managed forests are related to interspecific competition for limited roost sites, and to intraspecific division by sex that depends on local population numbers.

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## INTRODUCTION

Findley (1993) summarized relationships between bat morphology, diet, and ecological niches to define a bat community in attribute space. Using work of Findley and Wilson (1982), Findley and Black (1983), and Aldridge and Rautenbach (1987), Findley states “. . . it is possible to have a reasonable amount of confidence in the ability of morphology to provide an insight into the feeding and foraging of insectivorous bats. Bat reproduction, occurrence, and abundance are related to food abundance, and in that sense food is clearly limiting to animals.” Humphrey (1975), however, found a strong correlation between the diversity of physical structure and the diversity and richness of colonial bats. Perkins (1993) reported that the distribution of bat species in a nearctic managed forest is not random, and speculated that forest bat distribution is a result of roost availability, insect concentrations, or competition between species resulting in displacement. Perkins and Peterson (1995) concluded that the distribution of reproductive female bats in a managed forest was affected by availability of roosts. In areas where harvest of large, older trees was highest, statistical analysis indicated a significant over-representation of the largest bat species. In areas where timber harvest was non-existent or minimal, the only competition exhibited at foraging sites was between the three species that forage exclusively or primarily on moths (*Corynorhinus townsendii*, *Myotis thysanodes*, *Myotis volans*). In contrast, Bell (1980) reported no foraging competition between paired bat species at concentrated insect patches in similar forested and Great Basin habitat.

Here, I examine data regarding male and female distribution, prey, and roost selection in a managed forest. I hypothesized that (1) the males forage separately from females of the same species; and (2) the determinant of the presence of any paired species at foraging sites is not solely foraging competition, but also involves roost availability.

## STUDY SITE

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My study area is in northeastern Oregon on the Wallowa-Whitman National Forest (44° 44' to 46° 00'N, 116° 30' to 117° 45'W; Figure 1). I sampled 140 sites distributed arbitrarily throughout four ranger districts: Hells Canyon National Recreation Area, Wallowa Valley Ranger District, Eagle Cap Ranger District, and Pine Creek Ranger District. Over 486,000 ha (1.2 million acres) of public and private forest and canyons comprise the study area. Ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies grandis*) are the dominant tree species. I divided the study area into three habitat blocks, based on vegetation and management practices: Forest, Forest/Canyon Edge, and Canyon. Roost habitat surrounding Forest sample sites is limited to trees, snags, stumps, and a few buildings. This habitat comprises the largest area, had the most sample sites, and has had the greatest timber harvest in past decades. Roost habitat in the Forest/Canyon area included trees, snags, stumps, cliffs, talus, mines, and buildings. This was the second-largest sample area, had fewer sample sites, and the least impact in terms of timber harvest. Canyon habitat is not considered in this analysis.

I have recorded by capture or audible call signatures 13 species from the study area. Four of these species were not considered due to their low capture rates (*Lasiurus cinereus*, *Euderma maculatum*, *Corynorhinus townsendii*, and *Myotis yumanensis*).

## MATERIALS AND METHODS

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I sampled Forest and Forest/Canyon sites by setting mist nets over open water. Mist netting occurred from 1 June to 1 September 1984–1994. Netting periods lasted at least two hours after sunset. Bats were identified to species, sexed, aged, weighed, and morphological measurements were taken.

To test for division of foraging sites by sex, I used the chi-square test (Williams 1993). *Lasionycteris noctivagans* data are from Perkins and Cross (1992). To test for independence of distribution at foraging sites I paired each possible group of species and applied Fisher's exact test. Netability varies among species. To minimize this bias, I assigned a value for each species at each site as either present (1) or absent (0).

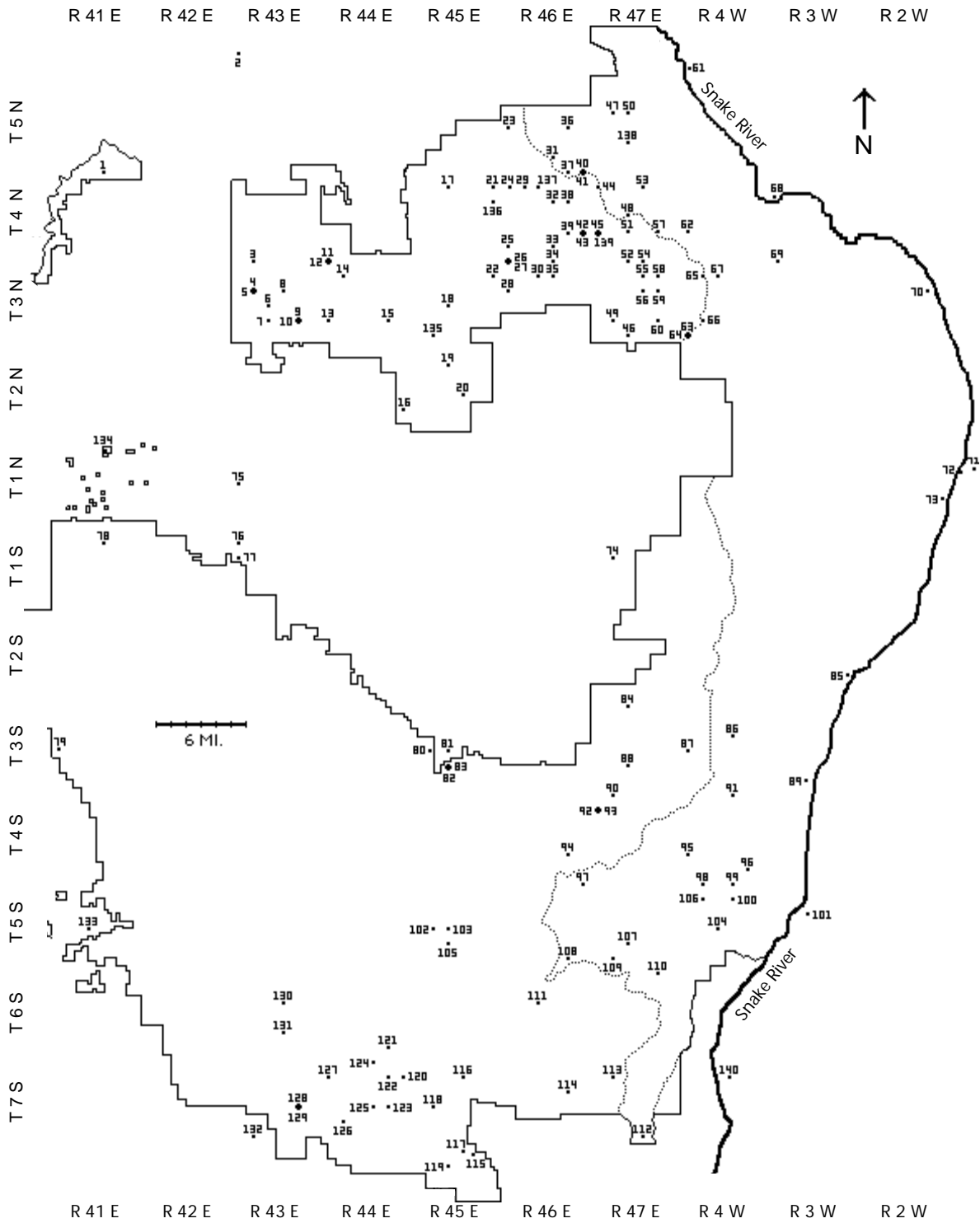


FIGURE 1 Study area, WWNF, Oregon, U.S.A. Thin line indicates forest boundary. East of the broken line is the HCNRA. Small dots represent single sample sites to nearest section. Large dots show two sites within section.

Chi-square analysis of exclusivity in male and reproductive female foraging patterns resulted in statistically significant separation between the sexes for all eight species for both portions of the study area, regardless of timber impacts (Table 1). However, Fisher's exact test indicates that when reproductive status is not considered, paired *M. californicus*, *M. ciliolabrum*, and *M. thysanodes* in both habitats had no foraging separation between the sexes. *M. californicus*, *M. ciliolabrum*, and *M. thysanodes* were the species that I captured the least of the eight considered. In the Forest/Canyon habitat, *M. evotis* and *M. lucifugus* also had no significant segregation by sex.

If we divide the bats into morphological sizes based on forearm length, skull size, and mass, we get a large bat group (*E. fuscus*, *L. noctivagans*), a middle-sized group (*M. evotis*, *M. volans*, *M. thysanodes*), and a small group (*M. lucifugus*, *M. ciliolabrum*, and *M. californicus*). The occurrence of large and small species together at sites was less than expected by chance in 67% (32 of 48) of the cases. Middle-sized bats and small bats were less frequently associated than expected in 73% (35 of 48) of cases.

In terms of foraging "style," gleaners (*M. evotis*, *M. thysanodes*) show competitive exclusion for both sexes. Forest and clearing aerial-insectivores (*E. fuscus*, *L. noctivagans*, *M. californicus*, *M. ciliolabrum*, and *M. volans*) produced mixed results indicating lower competition. In pairs of these species, 58% of cases indicated significant avoidance (29 of 50). *M. lucifugus* is the only water-surface forager, but significantly avoided other species in 68% of cases (19 of 28).

There was a slight difference in frequency of significant avoidance between the two habitats (when I excluded same species/different sex pairs). In the Forest habitat, competition was indicated in 70% of cases (74 of 105), while in the Forest/Canyon habitat competition occurred in 60% of cases (63 of 105).

## DISCUSSION

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My results indicate that the long-held assumption that sexes forage in separate areas is valid, particularly for the larger species, and those which form larger colonies outside of human structures. The lack of foraging habitat segregation by sex in the small and less numerous bat species (*M. californicus*, *M. ciliolabrum*, *M. lucifugus*, and *M. thysanodes*) suggests that prey biomass is not a critical factor in determining distribution or foraging sites when numbers of resident individuals are low.

Analysis of species pairs by sex seems to validate the concept of competition for foraging areas as a factor influencing distribution (Findley 1993). If one takes into account prey species and foraging techniques, it is difficult to imagine how *L. noctivagans* or *E. fuscus*, who forage at tree-top level at dusk, compete with *M. lucifugus*, *M. californicus*, or *M. ciliolabrum*, who forage low over meadows, water, in clearings, or under canopies in riparian zones. Whitaker et al. (1977) demonstrated that diets of



*M. californicus* and *M. lucifugus* only overlap with the middle-sized and large bat species in consumption of Diptera and Lepidoptera. *M. lucifugus* and *M. californicus* consume (by volume) mostly Diptera, while for large and middle-sized bats, Diptera make up less than 10% of consumed volume. Lepidoptera seem to be the prey common to all bat species represented on the study area. Prey analysis indicates that the small bat species eat less Lepidoptera by volume by at least a factor of two when compared with the larger bat species. Dietary competition is most likely to occur in consumption of lepidopterans: *L. noctivagans* (32% of prey volume), *E. fuscus* (21% of prey volume), *M. evotis* (46% of prey volume), *M. thysanodes* (46% of prey volume), and *M. volans* (78% of prey volume) (Whitaker et al. 1977; Whitaker et al. 1981). However, if prey competition is important, why is there inconsistent evidence of foraging competition between *E. fuscus* and *M. volans*, and between *L. noctivagans* and *M. volans*?

A close inspection of roosting behaviour provides the most likely answer. *E. fuscus*, *L. noctivagans*, and *M. volans* females all prefer abandoned woodpecker holes as maternity roosts, while males of these three species generally use crevices (Barclay 1985; Vonhof 1994; Kalcounis 1994; P. Ormsbee, pers. comm.). If roost availability is the determining factor in the significant differences in paired bat distributions, then female *L. noctivagans*, *E. fuscus*, and *M. volans* should rarely occur together. Indeed, my data suggest that this is the case. Other bat species of both sexes seem to rely mostly on crevices in cliffs and trees, or exfoliating bark, in the absence of human structures (Perkins 1993; Kalcounis 1994; P. Ormsbee, pers. comm.). If we assume that roosts adequate for *M. californicus* are also adequate for other crevice-roosting bats, I would expect that "might makes right," and the larger and more aggressive bat species out-compete the smaller and the less aggressive species.

Differences in the distribution of bats between the two habitats in the study area can be attributed to the greater harvest of trees in the Forest habitat. As well, in the Forest/Canyon habitat, alternate roost sites such as cliffs, caves, and human structures are more abundant than in the Forest habitat, thereby lessening competition. Perkins and Peterson (1995) noted potential foraging competition only among reproductive females of three bat species that are moth strategists (*M. thysanodes*, *M. volans*, and *C. townsendii*), and only in the Forest/Canyon habitat. Other significant differences noted in Tables 1 and 2 could be attributed to foraging interactions, but results here, and those of Perkins (1993), Perkins and Peterson (1995), Humphrey (1975), and Bell (1980) all agree that bat distribution is more likely dependent upon roost availability and interspecific competition for roosts rather than dietary competition. Sexual segregation in foraging areas occurs in most species, and may be correlated with local population densities of a given species.



## IMPLICATIONS

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If competition for roosts and roost availability is important in determining the distribution and success of bat species in nearctic forests, several questions arise:

1. Are present harvest practices especially harmful to smaller and less aggressive bat species?
2. Will future harvest practices result in lower population densities?
3. If competition for roosts is reducing populations of small and less aggressive species in the summer, what are the effects for species that depend on forest tree-roosts for hibernation?

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