USE BY BATS OF OLD-GROWTH REDWOOD HOLLOWS ON THE NORTH COAST OF CALIFORNIA

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Use by bats of basal hollows in old-growth redwoods was indexed using the weight of guano collected on water-permeable screens (guano traps) installed inside the trees. Twenty-six trees were systematically selected from a stand that flanks both sides of an interstate highway in Del Norte Co., California. Traps were checked for guano once a month for 18 months. The quantity of guano collected each month and that every tree was used suggests that the trees served either as day roosts by small numbers of bats or as temporary night roosts. Although bats could not be identified on the basis of characteristics of guano, three fecal morphotypes were identified. Guano was found in all 26 trees during most of the sample periods; the greatest deposition occurred May through August. Surprisingly, there was a substantial amount of fresh guano collected from most trees during winter months. When all trees were considered, weight of guano was not significantly related to diameter at breast height (dbh) of the tree during summer, winter, or annually, but was related to the internal volume of the hollow during summer and annually. Trees closer to perennial streams had greater weight of guano, but only during summer. The most frequently used trees had greater hollow volumes, greater diameters, and were closer to water than the least-frequently used trees. Although other potential roost sites on redwood trees were not sampled, our work indicates that large hollows are important roost sites. The relationship between weight of guano and size of hollow suggests that forests lacking trees large enough to contain these hollows will provide fewer roosting opportunities that could affect the abundance and diversity of bats.

Key words: bats, roosting, tree cavity, redwood

Basal hollows are interior cavities in living redwood (*Sequoia sempervirens*) trees that apparently are initiated when hot fires expose the heartwood (Finney, 1991). Subsequent fires and pathogenic agents cause the core of the tree to decay and a hollow to form. In mature and old-growth forests many of these "goosepen" hollows are >5 m in diameter, providing shelter for many species of animals. The value of hollows is magnified by their great longevity; redwoods can live 2,000 years (Becking, 1982) and hollows may be available during a significant proportion of this period.

When available, caves and mines are preferred hibernation sites, and sometimes locations of roosts for many species of bats (Christy and West, 1993; Kunz, 1982). However, cavities in trees and the underside of scaling bark frequently are used as roost sites during summer (Barclay et al., 1988; Brigham, 1991; Christy and West, 1993; Lunney et al., 1988; van Zyll de Jong, 1985). Especially because caves and mines are rare along coastal northern California

(Irwin, 1960), we hypothesized that hollows of old-growth redwood might be attractive roosts or hibernacula.

Fourteen species of bats are expected to occur in redwood forests, based on general distribution maps (Barbour and Davis, 1969) and specimens in museum collections. Twelve of these (*Myotis lucifugus, M. yumanensis, M. californicus, M. evotis, M. thysanodes, M. volans, Eptesicus fuscus, Plecotus townsendii, Antrozous pallidus, Tadarida brasiliensis, Lasionycteris noctivagans,* and *Euderma maculatum*) commonly roost in caves, crevices, or cavities of trees (Christy and West, 1993). One species, Townsend's big-eared bat (*Plecotus townsendii townsendii*), is a category two candidate for federal listing under the Endangered Species Act. Work conducted in riparian redwood communities in central California has demonstrated that bats occupied most basal hollows sampled (Rainey et al., 1992), and, recently, two radiotagged *P. t. townsendii* were tracked to hollows in an old-growth redwood community and a California bay laurel site (*Umbellularia californica*) at Point Reyes National Seashore (G. Fellers, pers. comm.). Therefore, we expect that basal redwood hollows may be important roost sites for cavity-roosting species of bats in the northern coast of California.

While basal hollows may be common in stands of old-growth redwoods, the stands in which they are found have become rare. Less than 5% of old-growth redwoods that occurred in California before European settlement remain today (L. Fox, in litt.). Species of animals, including bats, that depend on secure, enclosed roost and rest sites have lost considerable habitat in a relatively short time. Our work was initiated to understand the importance of old-growth redwoods to the community of bats at large and to assess the effect that habitat destruction has had on populations of bats. Here we determine the frequency that redwood hollows are used by bats, seasonal distribution of that use, and the attributes of hollow trees that receive the most use by bats.

Materials and Methods

Study area.—The research was conducted from spring 1992 to autumn 1993 in a coastal area 4.8 km S of Crescent City, Del Norte Co., California. The area is a sinuous 0.2 by 4.0 km right-of-way along US highway 101 comprised almost entirely of old-growth redwoods with many trees >500 years old, based on ring counts in adjoining areas (M. Moore, pers. comm.). Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and grand fir (*Abies grandis*) occur less commonly throughout the region. The study area is bordered by the Pacific Ocean on the west, coastal grasslands, freshwater ponds, and farmlands to the north, second-growth (25–75 years old) redwoods and Douglas-firs (*Pseudotsuga menziesii*) on private timberland to the east and to the south. Eight buildings (two inhabited homes and six vacant outbuildings) are located on the perimeter of the site.

Sampling of basal hollows.—Use of basal hollows by bats was indexed using the amount of guano deposited while bats roost (Anthony et al., 1981; Rainey et al., 1992). Because guano deposited on the ground is difficult to find and decomposes rapidly, we suspended a water-permeable screen (3M Weedblock) within hollows to catch falling guano. These guano traps were suspended 0.5–1.0 m above ground and tacked to the inside wall of the hollow.

The presence of roosting bats is not always indicated by presence of guano beneath the roost (Dalquest, 1947). When foraging conditions are poor and bats do not feed, they defecate less and guano is not a good index of abundance (Anthony et al., 1981). However, we have assumed that the amount of guano collected over 1 month is proportional to the use of the site by bats.

To select hollows for sampling, a parallel strip transect (0.1 by 4.0 km) was established immediately adjacent to both sides of highway 101. The strips were divided into 26, 75 by 100-m rectangular units. A single hollow-bearing live tree was selected within each unit based on the following criteria: the hollow should be as far from the unit edge as possible; be protected from disturbance by rain; have a ceiling height >2 m and hollow depth ≤0.5 m. In addition, trees were selected to attain a uniform distribution

among three classes of distance from road; 0–33, 34–66, and 67–100 m. Because density of potential sample trees appeared to decrease with distance from the road, the actual number of trees in each distance category, from closest to farthest from the road, was 12, 9, and 5. Twenty-six trees, 14 on the east side of the road and 12 on the west, were included in the sample.

Guano of bats was collected on 18 occasions, separated by ca. 1-month intervals from April 1992 through August 1993. Technicians were trained to distinguish feces of bats from feces of mice, rats, and birds. Some species and groups of species of bats are believed to have distinctive characteristics (M. Lacki, pers. comm.; E. Pierson, pers, comm.), but we did not attempt to distinguish species. Pellets of guano collected at each hollow, each month, were combined, oven dried (69°C for 2.5 h), and weighed (to the nearest 1 mg) within 24 h of collection. This weight became the index of use of hollows by bats and was the dependent variable for all analyses.

Analyses.—The initial analyses were conducted on the full dataset of 26 trees. Use of hollows by bats, as indexed by weight of guano, was analyzed on the basis of season, diameter of the hollow-bearing tree at breast height (dbh), internal volume of the hollow, distance to and seasonality of nearest water (perennial or ephemeral), and distance to highway. Diameter at breast height was measured around the complete circumference using a tape line. Volume of the internal hollow was calculated by estimating its depth, width, and height. Distance to water was determined by site reconnaissance and from United States Geological Survey, 7.5-min; quad maps; seasonal availability of water was recorded throughout the study during routine reconnaissance.

Data for all 18 monthly samples were combined in some cases, and in others were segregated by season. Summer corresponded to the dry season (April–September) and winter to the wet season (October–March). Data for winter are presented as the mean of 6 months of weights of guano for individual trees during the single winter season. However, weight of guano in summer was the mean of the two, 6-month summer periods that were included in the study. Regression and correlation analyses (SAS Institute, Inc., 1985) were used to assess relationships among average weight of guano, dbh, volume of hollow, and distance to water. Distance to highway and distance to and seasonality of the nearest watercourse to each tree were categorical variables that were analyzed using analysis of variance and *t*-tests, after testing for inequality of variances using *F*-tests. Data from all 26 trees were included in the analyses. The sample size was considered inadequate to conduct stepwise discriminant analysis to identify the relative contributions of independent variables (Johnson, 1981).

Highest versus lowest guano-producing trees.—Because we discovered that weight of guano was extremely variable among trees, we also compared characteristics of a subset of 12 trees from the full dataset for each season; six with the highest and six with the lowest average weight of guano. The mean of both summers (1992 and 1993) was used to rank trees for selection during the summer. The six highest guano-producing trees during summer were especially easy to distinguish from all other trees. Characteristics of the highest and lowest guano-producing trees were compared using the same independent variables listed above for the full ($n = 26$) dataset.

Results

All trees.—Each of the 26 hollows sampled had guano collected from the trap at some time during the 18-month period (Fig. 1). However, the incidence of occurrence of guano was greater in summer than in winter (Table 1). Mean weight of guano per hollow also was greater during summer than winter ($t = 2.88$, $P = 0.007$; Table 1; Fig. 1). Deposition of guano was greatest during May through June (Fig. 2) and was least from January through March. Individual fecal pellets averaged ca. 4 mg, resulting in an mean estimate of 34.2 (range = 0.6–147.4) pellets collected per hollow per month annually (Table 1).

Three morphotypes of guano were collected: small and black (ca. 5 by 2 mm), large and black (ca. 9 by 2 mm), and large and brown (9 by 3 mm). The small and large black feces were collected from every hollow at some time during the study, whereas the large, pale-brown feces were collected at only two hollows on a total of six occasions.

Weight of guano was not significantly re-

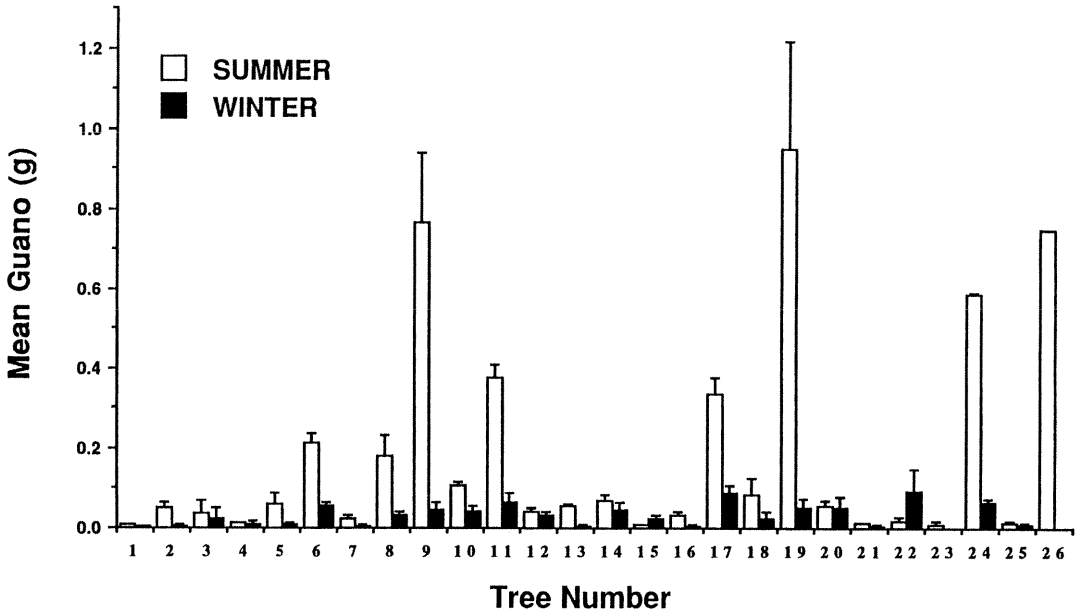

FIG. 1.—Mean (±1 SE) weight of guano for 18 months from 26 hollows for summer (April–September) and winter (October–March).

lated to dbh during summer ($R^2 = 0.13$, $P > 0.05$), winter ($R^2 = 0.06$, $P > 0.05$), or annually ($R^2 = 0.20$, $P > 0.05$). However, weight of guano was related to volume of hollow during summer ($R^2 = 0.40$, $P < 0.05$) and annually ($R^2 = 0.62$, $P < 0.05$). Although these relationships were influenced strongly by the deposition of guano in the largest-volume tree, they remained significant with this value excluded (summer, $R^2 = 0.42$, $P < 0.05$; annual, $R^2 = 0.44$, $P < 0.05$). Not suprisingly, volume of hollow and dbh are significantly, and positively, related ($r = 0.43$; $P < 0.05$).

Water was available in most streamcourses during winter, but was limited to larger creeks during summer. There was no relationship between distance of hollow to nearest watercourse and weight of guano during either season (winter, $R^2 = 0.0001$; summer, $R^2 = 0.06$). However, when availability of surface water in the nearest watercourse was considered, weights of guano were significantly greater, but during sum-

TABLE 1.—*Guano deposition in hollows by season. Numbers represent means (± 1SE) of 26 trees for the time period specified.*

Parameter	Summer			Winter	Total for sample period
	1992	1993	1992 and 1993	1992/1993	
Number of months	6	5	11	7	18
Percentage of months with guano	81.9 (4.2)	72.8 (5.5)	77.4 (3.5)	53.9 (6.3)	69.7 (3.4)
Weight of guano per hollow per month (g)	0.197 (0.06)	0.152 (0.05)	0.187 (0.05)	0.031 (0.005)	0.137 (0.034)
Number of fecal pellets per hollow per month[a]	49.2	38.0	46.7	7.7	34.2

[a] Weight of guano divided by 4 mg, the average weight of a fecal pellet.

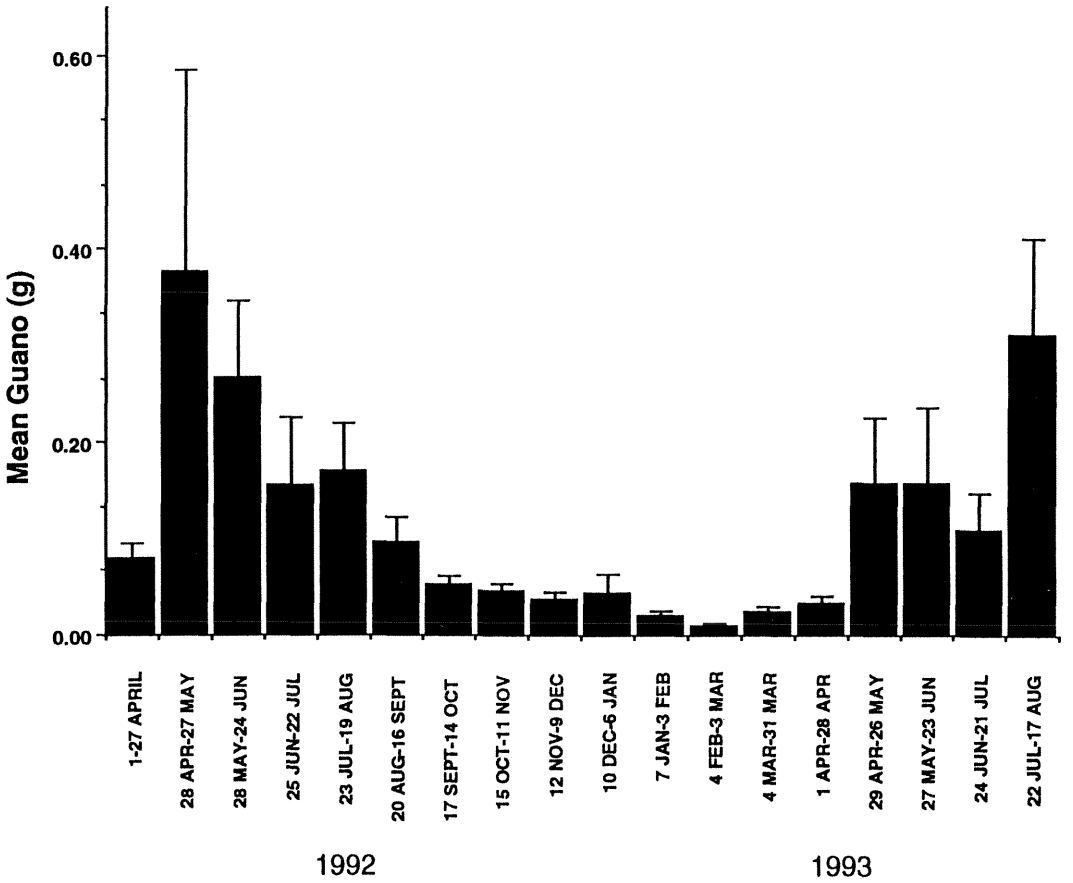

FIG. 2.—Mean (±1 SE) weight of guano from 26 trees for each of 18 ca. 1-month time periods, spring 1992–summer 1993.

mer only, in trees that were closer to perennial streams (where surface water was available) than trees that were closest to ephemeral streams ($t = 2.56$, $P = 0.02$; Fig. 3). The surface areas of the traps in these two classes of trees were no different ($t = 0.62$, $P = 0.53$). As expected, there was no difference during winter when most streamcourses contain water and when weights of guano were universally lower ($t = 1.02$, $P = 0.31$; Fig. 3). Although the sample was small, there was no obvious effect of presence of the highway on use of hollows by bats, because there was no difference in weight of guano from trees in different classes of distance ($F = 0.56$, $P = 0.57$; Fig. 4).

Highest versus lowest guano-producing trees.—The six highest and six lowest guano-producing trees were trees 6, 9, 11, 17, 19, 24 and 1, 4, 15, 21, 23, 25, respectively, during summer and trees 6, 11, 17, 19, 22, 24 and 1, 2, 13, 16, 21, 25, respectively, during winter (Fig. 1). Five trees (6, 11, 17, 19, 24) were among the six highest guano-producing trees during both seasons, whereas three trees (1, 21, 25) were among the six lowest guano-producers during both seasons. During summer, the six highest guano-producing trees had a mean of 0.625 g of guano, whereas the six lowest had 0.011 g. The corresponding values during winter were 0.069 and 0.004 g. Thus, the six highest guano-producing trees had 56.8

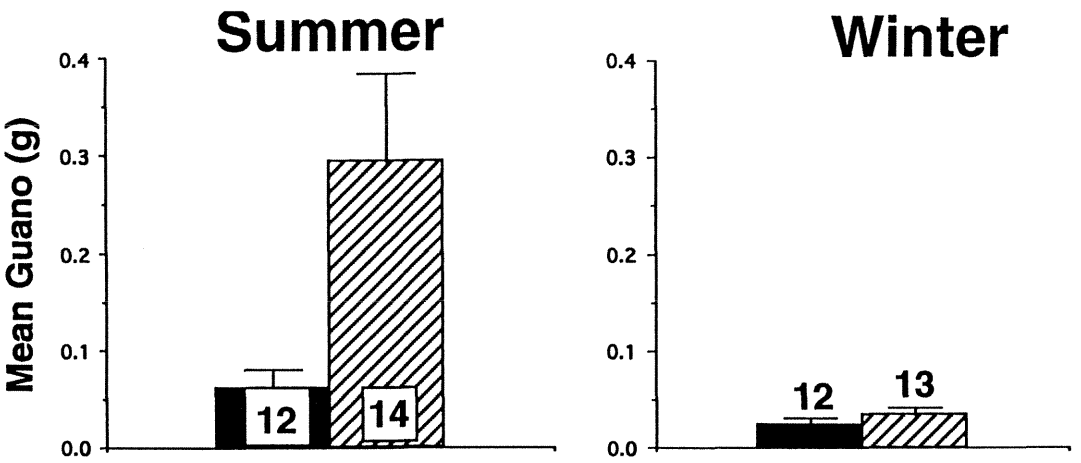

FIG. 3.—Mean (±1 SE) weight of guano for hollows closer to ephemeral (solid bar) or perennial (cross-hatched bar) water. Sample sizes are imbedded in, or above, bars.

and 17.2 times as much guano as the six lowest, in summer and winter, respectively.

During summer, when use of hollows by bats was greatest, the six highest guano-producing trees had significantly greater diameters and greater volumes of hollows than the six lowest guano-producing trees (Fig. 5). The fact that bigger trees produced greater gross weights of guano than the smaller trees suggests that larger-diameter trees either attract more bats, or the same number for longer durations, than smaller trees. The volume, but not dbh, remained a significant attribute during winter as well.

Distance to road did not differ when high and low guano-producing trees were compared (Fig. 5). Although distance to watercourse did not significantly affect weight of guano during summer or winter (Fig. 5) when availability of water in the streamcourse was considered, five of the six highest guano-producing trees were closer to perennial than ephemeral streams and only two of the six lowest guano-producing trees were closer to perennial ones.

Many factors interact to affect occurrence of bats in hollows. While our data are not adequate to conduct multivariate analyses, it is helpful to realize that dbh is related to both volume of hollow ($r = 0.43$, $P = 0.02$) and distance to watercourse ($r = 0.11$, $P = 0.08$). Any relationship between weight of guano and dbh may, in part, be attributable to the larger trees having larger internal volumes and being closer to water than smaller trees.

DISCUSSION

One of the most striking results of the study was that every tree we sampled received some use during the year. This result is similar to that reported by Rainey et. al (1992), who studied deposition of guano from July to December in 24 riparian redwood hollows in the central coast region of California. Because the majority of trees had amounts of guano that were relatively low (mean monthly deposition ca. 50 fecal pellets during summer) and all trees received some use, the large hollows we sampled were used either as day roosts by few individuals or as temporary night roosts (Anthony et al., 1981; Cross, 1965; Dalquest, 1947; Hirshfeld et al., 1977).

Rumage (1979) calculated that a pregnant *M. lucifugus* produced 18 mg (dry weight) of feces h. Using this as an estimate of the production rate of feces in the hollows, the mean monthly weight of guano per hollow during summer results in an estimate of 10-11 bat hours of use per hollow per month. Using the maximum monthly

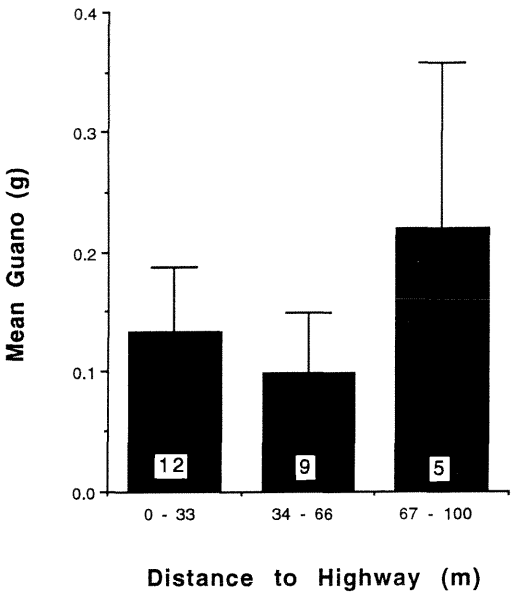

FIG. 4.—Mean (±1 SE) weight of guano from trees either 0–33, 34–66, or 67–100 m from the highway. Sample sizes are imbedded in bars.

weight of guano recorded for any tree results in an estimate of ≤50 bat hours month. This weight of guano could be produced, e.g., by only 10 bats residing in the hollow for only 5 h during a month (less if the species that occupy the hollows are larger than *M. lucifugus* and have heavier feces) and suggests that regardless of whether they are day or night roosts, bats probably are using individual trees infrequently.

Because we sampled a small number of the hollow-bearing trees in the area we may have overlooked nearby roosts that received more intensive use. It also is possible that bats were using roost sites other than basal hollows as day and maternity roosts. Size, morphology, and age of redwood trees afford an enormous variety of roosting choices other than basal hollows, including hollows with access other than at the base, deep internal fissures and crevices, and superficial external crevices in the bark.

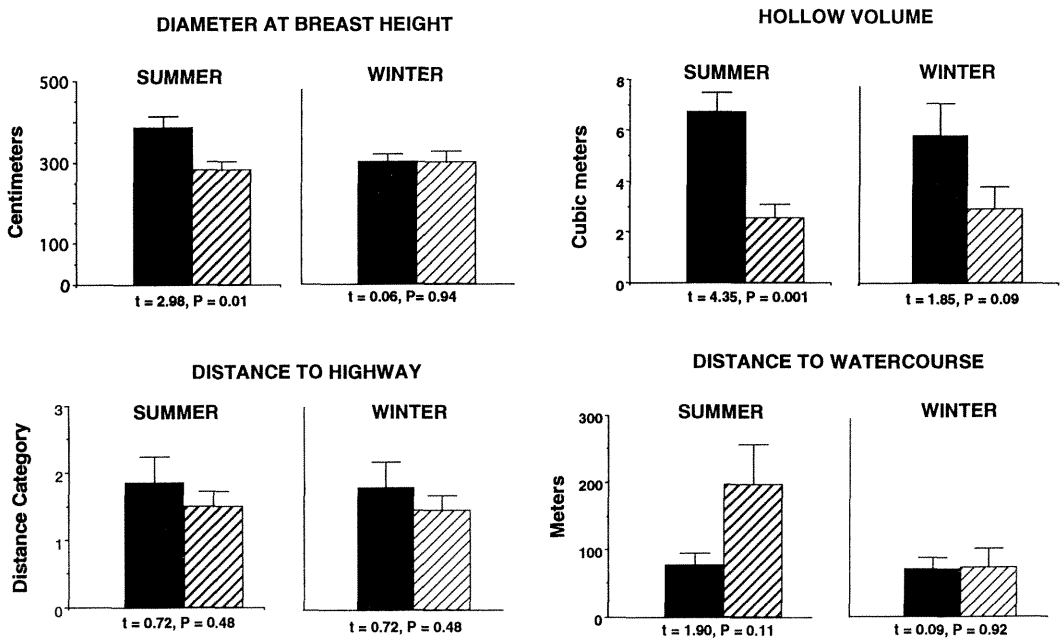

FIG. 5.—Comparisons between the six highest guano-producing trees (solid bars) and the six lowest guano-producing trees (cross-hatched bars) in regard to diameter at breast height, hollow volume (width by depth by height), distance to highway (category 1 = 0–33 m, 2 = 34–66 m, 3 = 67–100 m), and distance to watercourse.

None of the trees we sampled contained volumes of guano that indicated large nursery aggregations. However, a redwood tree ca. 10 km from our study area housed ca. 60 *M. yumanensis* (S. Gellman, pers. obser.) and W. E. Rainey et al. (pers. comm.) found a nursery colony of >500 of the same species in a large hollow redwood tree near Carmel, California. Small, day-roosting, reproductive units of *Myotis* and *L. noctivagans* (Parsons et al., 1986) could have been responsible for some of the higher weights of guano in summer. Although no bats were observed in hollows when traps were checked and cleaned, non-volant young (*Myotis*) were discovered on guano traps on two occasions during a subsequent study. Also, individually roosting males could have been using trees as day roosts (*M. yumanensis*—Dalquest, 1947). Nonetheless, we were surprised to find that none of the trees we sampled appeared to host maternity aggregations during summer, in contrast to the work of Rainey et al. (1992). Because night roosting is flexible behavior that varies with reproductive status and foraging success (Anthony et al., 1981; Dalquest, 1947; Krutzsh, 1954), it is likely that the low and variable nature of deposition of guano in the hollows we sampled reflects this activity.

Appearance of new guano during each winter month suggests that either resident bats are active during winter or that bats are taking temporary refuge in trees on the study site as they migrate through the area (Barclay et al., 1988). Of the species believed to migrate along the coast ranges and Cascade Range (i.e., *L. noctivagans, L. cinereus, T. brasiliensis*—Findley and Jones, 1964; Griffin, 1970; Perkins and Cross, 1988; Shump and Shump, 1982), none is known to commonly use tree hollows as roost sites (Barclay et al., 1988; Shump and Shump, 1982). *L. noctivagans* typically roosts in crevices, but its use of hollows has not been established. Thus, we assume that most of the guano collected during winter was produced by a resident population dominated by *Myotis*. Netting at another study site revealed that *M. yumanensis* is the most common bat captured during summer. Although *Myotis* is commonly observed during winter, its incidence of capture decreases during autumn and winter. Conversely, captures of *L. noctivagans* increase during autumn, and it is the most common bat captured during November through January. Both species appear to be active in the vicinity of the study area during winter. *P. townsendii* also is known to be active during winter in coastal California (Pearson et al., 1952).

When all trees are included in the analysis there is no relationship between use by bats (as indexed by weight of guano) and dbh of the tree, contrary to the work of Rainey et al. (1992). However, when the highest guano-producing trees are compared to the lowest, dbh distinguishes the two classes. Volume of the hollow has a consistent positive relationship with weight of guano for both analyses during summer. Perhaps large volumes provide more flight space or permit access to a greater variety of protected microsites for roosting. It also is likely that larger hollows have more favorable microclimates because choices of roosts elsewhere are influenced by temperature and humidity (Anthony et al., 1981; Kunz, 1982). Internal volume of hollows also may help explain why the relationship between dbh and weight of guano was poor for the full dataset. A number of large-diameter trees had narrow hollows with small volumes; if large internal volume attracts use by bats then we would not expect a strong linear relationship between dbh and weight of guano.

Roosts frequently are found in proximity to water (Brigham et al., 1992; Fenton et al., 1980; Herd and Fenton, 1983; Kunz, 1982; Thomas, 1988). Because the study area was relatively wet year-round, it was somewhat surprising to find that during summer, trees closer to surface water had evidence of more use by bats. However, summer moisture is available primarily as

dew from fog and may not be readily available to bats, thus bats may choose sites that minimize the distance from roosts to surface water where they drink and forage.

The nearby disturbance of a large highway had no apparent effect on use of hollows by bats. Trees as close as 8 m to the right-of-way had some of the highest monthly weights of guano recorded. It is possible that the highway provides a convenient corridor compared to the closed canopy of the forest. However, any conclusion is premature because our small sample and the multivariate nature of choice of roosts lowered the statistical power of our test, we were not monitoring maternity roosts, which a previous study found occured farthest of all roosts from roads (J. E. Gardner et al., in litt.), and it is possible that all trees in our sample were too close to the road and received universally low use by bats.

We measured a number of the most obvious variables that could influence use of hollows by bats, but failed to consider many others. We did not record data on microclimatic variables and are certain that these influence choice of roost sites. Basal hollows that have low interiors probably do not receive direct sunlight and are cool year-round, making them less likely maternity sites than cavities near tops of trees that probably are much warmer (Fenton and Barclay, 1980). We also did not characterize the environment immediately surrounding the hollow. Gaisler et al. (1979) found that trees used as roosts by *Nyctalus noctula* had few branches below the main crown and space for free flight in front of the entrance. Thus, it may be possible that entrances to basal hollows in redwoods obstructed by the often thick, evergreen, shrub by understory (e.g., *Gaultheria, Vaccinium*) receive less use than those that are not.

Three morphotypes of guano were collected; small black feces, large black feces, and large pale-brown feces. The small black feces were the most common and most probably were from *Myotis* (E. Pierson, pers. comm.). Large black feces were fairly common and were most likely deposited by *L. noctivagans* and *E. fuscus.* The pale-brown feces were found in two hollows and their paler color probably is attributable to scales of moths (E. Pierson, pers. comm.; M. Lacki, pers. comm.). *P. townsendii, L. noctivagans, M. evotis,* and *M. volans* all eat moths in the Pacific Northwest (Whitaker et al., 1977; 1981*a,* 1981*b*). Identification of bats by their feces was beyond the scope of this project, but it seems possible that a multivariate approach using size, external morphology, and remains of prey (developed using feces from captive bats fed natural diets and feces produced by bats captured in the field) could be successful. Alternatively, thin-layer chromatography of bile acids (Major et al., 1980) or analysis of DNA (Hoss et al., 1992) may eventually be capable of solving the feces-to-species question. If the identity of feces could be determined, collection of guano from basal hollows could become a useful tool for understanding ecology of bats and indexing abundance of populations.

Identification of feces would be especially helpful in identifying areas inhabited by *P. townsendii* because this species is infrequently trapped in mist nets at streams (M. Perkins, pers. comm.); produces ultrasound vocalizations that are difficult to detect (W. Rainey, pers. comm.); and, as a candidate for federal listing, is a species for which we need more information. *P. townsendii* has been documented in redwood forests ca. 120 km south of our study area (S. Gellman, pers. obs.), and a radiotagged individual roosted in a hollow redwood at Point Reyes National Seashore, California (G. Fellers, pers. comm.). It is likely that this species may soon be found in roosts in our study area. Although the species is believed to roost primarily in caves, mines, and other cave-like human structures in California and Oregon (Marcot, 1984; Perkins and Levesque, 1987; Pierson et al., 1991), its use of trees may be underestimated.

Although many species of bats in the Pa-

cific Northwest use caves as hibernacula and sometimes as summer roosts, caves are uncommon in coastal redwoods, and old redwoods probably share some of the same characteristics as caves. These trees have relatively stable temperatures and humidity, pronounced light gradients, protection from rain, spacious internal flight areas, and are long-lived. Unfortunately, logging of old-growth redwood forests has resulted in few remaining areas with large, old redwood trees. Availability of roost sites in young, second-growth trees has not been evaluated, but these trees rarely have basal hollows. Studies in other types of forests have demonstrated that unlogged forests have greater activity of bats (Thomas, 1988) and more trees with preferred roosts (Lunney et al., 1988) than second-growth forests. Moreover, areas with a limited array of roosts usually have a less diverse fauna of bats (Humphrey, 1975). The relationship between large volume of internal hollow and use by bats suggests that forests lacking trees large enough to contain these hollows, and lacking caves, provides fewer roosting opportunities and potential hibernacula; a result that could affect abundance and diversity of bats.

Large basal hollows are not exclusively a feature of redwood trees; in California they also occur in incense cedars (*Calocedrus decurrens*), Douglas-firs (*Pseudotsuga menziesii*), and giant sequoias (*Sequoiadendron giganteum*), among other species. Compared with other roosts in trees, basal hollows are easy to sample for evidence of bats. Modifications of mist-netting techniques and use of ultrasound detectors and radiotelemetry will enhance our knowledge of bats using these roosts. The potential importance of tree cavities in the ecology of bats in temperate forests should not be underestimated. Responsible management of forests dictates that studies of the natural roost sites of bats in forests (basal hollows, other cavities and crevices, and foliage) should not be overlooked in favor of artificial sites (e.g., mines, buildings) that may be easier to locate and where bats are easier to study.

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