Bat Use of Remnant Old-Growth Redwood Stands

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Abstract: *Most of the old-growth redwood (*Sequoia sempervirens*) in California has been cut; regenerating forests will probably never resemble those that were harvested, and what old growth remains on private land occurs in small, isolated remnant patches. The landscapes in which these stands occur differ so markedly from their original condition that their value as habitat to many species of wildlife, including bats, is unknown. Previous research in unfragmented redwood forests demonstrated that bats use basal hollows in old-growth redwoods as roosts. We sought to determine whether bats use similar old-growth trees as roosts when they occur in small, remnant patches of isolated old growth on commercial forest land. We compared bat occurrence in remnant and contiguous stands by collecting guano in traps suspended in hollows and by monitoring flight activity with ultrasonic bat detectors. Hollows in trees within the remnant stands had significantly more guano deposited per tree than the trees within the contiguous forest. The mean numbers of bat passes per night were statistically indistinguishable between the two treatments, although mean flight activity in the remnant stands was greater than in the contiguous forest. Bats frequently used basal hollows in small (<5 ha) stands of remnant old growth, which may be due to the closer proximity of remnants to stream courses, to their greater interface with edge where foraging success may be greater, or to the fact that the lower density of hollow-bearing trees in remnants than in contiguous forest favored greater use per tree. Significant use of small, residual old-growth redwood provides reason to maintain these remnants in managed landscapes as potentially important habitat for forest bats.*

Uso de Remanentes de Bosques Maduros de Secoyas por Murciélagos

Resumen: *La mayoría de los bosques maduros de secoyas (*Sequoia sempervirens*) de California han sido talados, los bosques en regeneración quizá nunca sean lo que alguna vez fueron los bosques talados y lo que queda de bosque maduro en propiedades privadas ocurre en parches remanentes pequeños y aislados. Los paisajes en los cuales estos remanentes ocurren difieren tan marcadamente de las condiciones originales que su valor como hábitat para muchas especies de vida silvestre, incluyendo a los murciélagos es desconocido. Investigaciones previas en bosques no fragmentados de secoyas demostraron que los murciélagos utilizan huecos en los árboles como perchas. Intentamos determinar si los murciélagos usan árboles similares a los utilizados en bosques maduros cuando estos ocurren en parches de bosque maduro pequeños y aislados en tierras forestales comerciales. Comparamos la presencia de murciélagos en sitios remanentes y en sitios contiguos mediante la colección de guano en trampas suspendidas en agujeros y por monitoreo de la actividad de vuelo mediante detectores ultrasónicos de murciélagos. Los agujeros en los árboles dentro de los sitios remanentes tuvieron significativamente mas guano depositado por árbol que los árboles dentro de bosques contiguos. El número promedio de murciélagos que pasaron por noche fue estadísticamente indistinguible entre los dos tratamientos, aunque la actividad promedio de vuelo en los bosques remanentes fue mayor que en los bosques contiguos. Los murciélagos frecuentemente utilizan agujeros basales en porciones remanentes pequeñas de bosque maduro (<5 ha), lo cual puede deberse a la cercana proximidad de los remanentes a los cauces de arroyos, su gran interface con el borde donde el éxito de forrajeo debe ser mayor, o al hecho de que la densidad baja de árboles con agujeros en las bosques remanentes favorece un mayor uso por árbol. El uso significativo de pequeños bosques residuales maduros de secoyas provee una razón para mantener estos remanentes en paisajes manejados como un hábitat potencial para murciélagos de bosque.*

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Introduction

With the exception of extensive stands that may occur in reserves such as national parks, remnant patches are about all that remain of the original forest cover that preceded European settlement in the United States. Approximately 85% of the primary forests in the United States and 95–98% of those in the conterminous 48 states have been harvested (Postel & Ryan 1991). The result has been an increase in the number of forest fragments, amount of edge, and isolation of remnant forest patches (Groom & Schumaker 1993). In many cases, small patches of original forest are all that remain as examples of particular vegetation types (Groom & Schumaker 1993; Saunders et al. 1993). These scattered forest remnants cannot function as ecological entities. Thus, it is the modified landscapes that must be managed to retain the full complement of species adapted to the older and more contiguous forests of the past. Remnants are the obvious nuclei on which to base the restoration of mature forests. Because more effort is being directed toward the management and preservation of forest remnants, it is necessary to determine how remnants function to provide habitat to the wildlife species they are intended to benefit.

Previous work has focused on the relationship between stand age and indices of bat abundance, and the result is the nearly unanimous conclusion that older forests favor abundant and diverse communities of forest bats (Thomas 1988; Fenton et al. 1992; Huff et al. 1993; Krusic et al. 1996; Parker et al. 1996). Our interest is different: we sought to understand how bats use old trees in small remnant patches of old growth versus old trees in contiguous, unfragmented forest. This information may help managers assign value to the increasingly rare patches of old (>500 years) redwood forest within the extensive matrix of younger stands (5–80 years old) in the north coast of California.

Basal hollows in redwood trees are important roost sites for bats in coastal northern California. Hollows form as the result of periodic fires and subsequent wood decay (Fritz 1932; Finney 1996) and can become very large and persist for centuries before the tree falls. Forest-dwelling bats use the fire-scar cavities in redwood as maternity, day, and night roosts and occupy hollows during every month of the year (Rainey et al. 1992; Gellman & Zielinski 1996). Trees with the largest hollow volumes and those nearest to available surface water appear to receive the greatest use by roosting bats (Gellman & Zielinski 1996). Our previous work in the redwood forest of the north coast of California was conducted exclusively in a reserve (Redwood National Park and associated state parks), and sample trees were selected from among many in a large, contiguous block of original forest. These forests are rare across the range of redwood; less than 10% of the range of redwood is occupied by large patches of dense, old-growth redwood forest (Fox 1996). Most of the redwood region is privately owned, has been logged, and exists as young, second- or third-growth forest. Old-growth forest that occurs outside the boundaries of federal and state parks does so in the form of small, remnant stands that punctuate the landscape of young forest. These small stands are increasingly valued by wildlife managers for the unique and rare elements they provide—large and sometimes hollow live trees, large snags, large logs—and by environmentalists who wish to protect original forests that are not currently in reserves.

With the knowledge that bats use hollows in old-growth redwood forests, we became interested in determining whether this use was influenced by the type of stand in which the hollow-bearing tree occurred. For instance, were trees with basal hollows in contiguous old-growth forest used more often than similar trees in small, old-growth "islands" surrounded by forests regenerating from harvest? It is commonly assumed that these small stands are so rare as to contribute little habitat value in the region and, consequently, there have been few efforts to protect them outside of federal reserves. Recently though, small "set-asides" for Northern Spotted Owls (*Strix occidentalis caurina*) and Marbled Murrelets (*Brachyramphus marmoratus*) have begun to be considered in habitat conservation plans developed by private companies in the redwood region (Simpson Timber Company 1992). Whether these set-asides should include remnants of original old-growth forest is still a matter of debate (A. Brickey, personal communication).

We conducted a study to compare the use by bats of hollow, old-growth redwood trees in contiguous forest and in remnant stands to determine the importance of these increasingly rare landscape features to the community of forest bats in the northern coastal region of California. We compared indices of roosting behavior and flight activity to evaluate how bats use the remnants of the forests that preceded European settlement.

Methods

Study Area

The work was conducted from the spring of 1992 through the autumn of 1994 in the California Coast Range, approximately 16 km south of Crescent City, Del Norte County, California (Fig. 1). The contiguous forest study area was an approximately 1300-ha portion of Del Norte Coast Redwood State Park, which adjoins and is managed cooperatively with Redwood National Park. Most of this part of the study area was within 2 km of the ocean and was primarily old-growth redwood forest, with most mature trees exceeding 500 years of age. Sitka spruce (*Picea stichensis*), western hemlock (*Tsuga heterophylla*), grand fir (*Abies grandis*), and Douglas fir (*Psuedotsuga menziesii*) were less common species in redwood-dominated stands. Red alder (*Alnus rubrum*) occurred along most of the streams

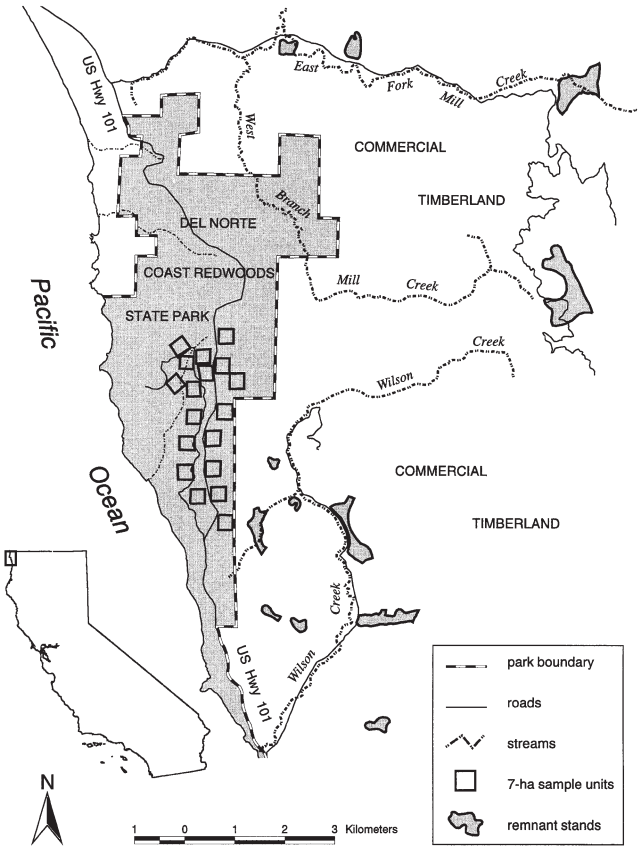


Figure 1. Study area, Del Norte County, California, depicting the spatial relationship between contiguous forest in the park and remnant stands (irregular polygons) in commercial timberland.

that drained the study area. Wilson Creek was the largest stream in the area.

The 12 remnant stands in our study represented most of those stands greater than 1 ha that remained within a large area of private land east and 2–5 km inland of the sample units in the park (Fig. 1). Remnants ranged in size from 1.9 to 56.3 ha (mean = 18.8 ha). All occurred within a matrix of second- and third-growth forest (20- to 80-year-old redwood and Douglas fir) on commercial timber-producing land. The remnant stands ranged from 0.2 to 4.8 km (mean = 1.9 km) from the boundary of the contiguous old-growth forest in the park (Fig. 1). The combined area that included all the remnant stands and the contiguous forest in the park totaled about 6000 ha.

Trapping

Because little research had previously been done on bats in this region of California, we conducted mist-net surveys at nine locations along Wilson Creek to establish a list of species that may roost in the vicinity. From one to nine nets (12 m and 6 m) were established along a 50-m reach of stream at each of nine locations along 5 km of Wilson Creek. Nets were opened about 0.5 hours prior to sunset and kept open for 3 hours or until at least 1 hour transpired without a bat capture at any net. All captured bats were banded and less than 2% were recaptured. Sampling occurred at each of these locations from one to five times from 12 May 1993 to 9 March 1994.

Guano Sampling in Hollow Trees

Guano was sampled by collecting it on water-permeable, black plastic screen suspended within large trees with basal hollows (Gellman & Zielinski 1996). Only trees with basal hollows were sampled. Beyond the recognition of three morphotypes of bat guano (Gellman & Zielinski 1996), we were unable to identify the species of bats using the hollows. Therefore, our study was unable to address the effects of landscape composition on the diversity of bats or on individual species. Sample trees were selected from the contiguous forest in the park by dividing its southern portion into 7-ha blocks (the approximate modal size of the remnant stands) and randomly selecting 18 of these blocks. Each block was traversed along transects spaced 50 m apart to locate trees with basal hollows. Three of these were randomly selected, with the constraint that trees within a block had to be at least 50 m apart and 50 m from the perimeter of the block. Fifty-four trees from 18 blocks composed the sample from the contiguous forest.

From two to five hollow-bearing trees were selected from each remnant stand, depending on its size, resulting in a total of 45 sample trees in remnant stands. Three trees were selected from stands 7 ha or smaller, except for two small stands that contained only two suitable trees. Five trees were selected from stands greater than 7 ha (range 7.4–23.5 ha). When field reconnaissance determined that there were more hollow-bearing trees in a stand than were necessary to sample, the required number for each stand was selected at random. Guano traps were installed in the first week of June 1993 and checked once a month through January 1994. Guano was oven-dried (69° C for 2.5 hours) and weighed (to the nearest 1 mg) within 24 hours of collection.

Because previous work demonstrated a relationship between both the diameter at breast height (dbh) and the internal volume of the hollow and the use of the tree by bats (Gellman & Zielinski 1996), we collected data on these variables from each tree we sampled. Hollow volume was the product of its height, depth, and width. Transects walked during the process of selecting trees to sample also produced estimates of the availability of trees with basal hollows deemed suitable for bat use. A team of assistants walked parallel transects such that all trees of sufficient size to contain a hollow were located and examined. This complete census was conducted in 11 of the sample units in the contiguous forest and all 12 of the remnant stands.

Remote Ultrasound Sampling of Flight Activity

We used remote ultrasonic bat detectors (Anabat II, Titley Electronics, Australia) to monitor the activity of bats in the vicinity of 47 of the same hollows where guano was sampled (23 in 12 remnant stands and 24 in 15 of the contiguous forest sample units) (Hayes & Hounihan 1994). Detectors were placed 1 m off the ground and about 5 m from, and oriented toward, the entrance to the hollow. Although we hoped bats emerging from or returning to hollows would be detected by the recorders, we viewed the method as a means for sampling general flight activity near the forest floor. Each unit included a photosensitive switch to turn the unit on at dark, a tape delay, a cassette tape recorder, and a 12V gel cell battery. Sufficient tape and battery power were available to record throughout the night, although most activity occurred in the hours shortly after sunset. An attempt was made to record bat activity for three consecutive nights at each sampling location, although at a minority of sites only two nights of data were collected due to detector malfunctions. On each sample night, ultrasound was sampled at an equal number of trees in remnant stands as in contiguous forest, so as to minimize confounding site effects with temporal effects on bat activity.

One observer listened to all tapes and tallied the number of bat "passes" (Thomas 1988; Krusic et al. 1996; Hayes 1997), which included all bat vocalizations (search phase, approaches, and feeding buzzes). The observer was trained to distinguish the vocalizations of bats from other ultrasonic sources by recording and studying the vocalizations made by various species of bats released by hand after capture. No attempt was made to distinguish the species of bats or the types of vocalizations (e.g., search phase from feeding buzzes).

Analysis

Prior to analysis, the data were assessed for departure from normality. Both the guano and ultrasound data were analyzed by a nested analysis for unbalanced data (PROC GLM in SAS, Inc.). Individual hollow trees were treated as replicates within stands, which were nested within treatment (contiguous or remnant stand type). The seven monthly guano weights were treated as replicates within a tree. For the ultrasound analysis, the mean number of bat passes over consecutive nights at a site was used to represent bat activity at the sample point.

Results

Trapping

One hundred and forty-two individual bats, identified to seven species, were captured during 16 nights, for a total of almost 260 net hours (Table 1). *Myotis yumanensis*, a crevice- and cavity-roosting bat (Dalquest 1947; Rainey et al. 1992), was the most frequently captured species and was captured most commonly during the summer. *Lasionycteris noctivagans*, which also roosts in tree cavities and crevices (Parsons et al. 1986; Barclay et al. 1988; Campbell et al. 1996), was infrequently captured during the summer, but males in particular comprised a substantial portion of the fall captures. Few bats were captured during the winter, although previous work has demonstrated a considerable amount of activity by bats during the winter months in this coastal environment (Gellman & Zielinski 1996).

Characteristics of Sampled Trees

The mean (SD) dbh of trees in the sample units within the contiguous forest and the remnant stands was 295.9 (82.0) cm and 271.2 (86.6), respectively (not statistically different, $F = 1.00$, $p = 0.32$). Trees in the contiguous forest had larger interior hollow volumes (mean [SD] = 25.5 [4.9] and 10.73 [4.8] m^3, respectively), but the difference was also statistically indistinguishable ($F = 2.78$, $p = 0.102$).

Wilson Creek was the largest stream course in the study area, and the sample units and remnant stands were not

Table 1. Seasonal distribution of the number of bats (male:female) captured in the mist nets on Wilson Creek, Del Norte County, California, 12 May 1993–9 March 1994.

Genus and species	*May–June*	*August–October*	*November–March*	*Total*
Myotis yumanensis	53 (32:21)	11 (9:2)	0	64
Myotis californicus	7 (3:4)	5 (5:0)	0	12
Myotis evotis	1 (0:1)	0	0	1
Myotis volans	0[a]	1 (1:0)	0	1
Lasionyteris noctivagans	7 (6:1)	42 (40:2)	7 (4:3)	56
Lasiurus cinereus	0	1 (1:0)	2 (2:0)	3
Eptesicus fuscus	2 (2:0)	3 (1:2)	0	5
Number of net hours[b]	99.5	64.9	94.8	259.2
Number of nights trapping	9	4	3	16

[a] *One female captured in tree hollow.*
[b] *One net hour means one 6-m net in place for 1 hour.*

equidistant from this source of food and water for bats. Remnant stands were significantly closer to Wilson Creek than the sample units in the contiguous stand (mean minimum distance = 304 and 1610 m, respectively; $t = 7.0$, $p < 0.00001$).

Hollow-bearing trees were significantly more common within the sample units in the contiguous forest (mean = 1.99/ha) than in the remnant stands (mean = 0.52/ha) ($t = 3.85$, $p = 0.002$). Thus, potential roost trees were more readily available in the unfragmented forest than within the patches of residual old growth.

Guano Deposition and Flight Activity

The mean (SD) amount of guano deposited was 0.89 (1.43) g per month per tree in the remnant stands and 0.38 (0.69) in the contiguous stands, with the biggest difference between treatment groups occurring in the month of June (Fig. 2). Accounting for the nesting of sample period within tree, tree within stand number, and stand number within treatment, the hollow trees within the remnant stands had significantly more guano deposited per tree than the trees within the contiguous, parkland forest ($F = 4.95$, $p = 0.035$).

Based on the mean of the multiple-night sample for each tree averaged over all trees per stand, the remnant stands averaged 10.02 passes per night, whereas the contiguous forest sample units averaged 7.80 passes per night (Table 2), a difference that was not statistically significant ($F = 1.00$, $p = 0.33$). Power would undoubtedly have been increased with additional samples, given the relatively large variances around each mean: 56.07 and 61.40, respectively. Six sample locations recorded a mean number of passes per night that exceeded 20, two of which were in remnant stands and four in contiguous stands.

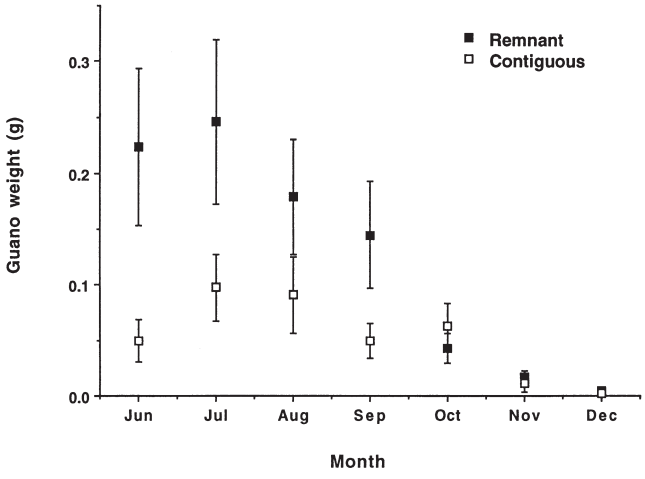


*Figure 2. Mean weights of guano collected from hollows sampled in remnant stands (*n *= 45 trees) and in the contiguous forest (*n *= 54 trees) from July 1993 to January 1994 in Del Norte County, California. Traps were checked the first week of every month, so the monthly data represent guano deposited from the first week of that month to the first week of the following month.*

Discussion

The guano data demonstrate a significantly greater use of old-growth trees in residual stands than within the contiguous forest. This suggests that either more bats use each of these trees or individual bats return to use these trees more frequently than they do trees within the unfragmented forest in the park. Although the ultrasound data were not statistically different, the isolated stands also had a higher index of bat activity (passes per night). It is clear that bats are making significant use of old-growth remnants, which make up a small proportion of the landscape.

Little is known about the dynamics of bat use of redwood forests and forest remnants. Our work was not designed to determine the origin and movements of the bats that used the stands we sampled. It is therefore possible that, given the abilities of some species to travel considerable distances (Morrison 1979; Wilkinson 1985; Brigham 1991; de Jong 1994), the bats we detected in the remnants may at times commute between the remnants and the larger, intact forest in the park. The areas between the remnants and the contiguous forest had few old trees but were probably not entirely hostile to bats because they were composed of regenerating redwoods and hardwoods that in some areas provided dense cover

Table 2. Mean number of bat passes per night, averaged across the trees within each stand, for sample sites within remnant stands and sample units within contiguous forest.

Stand or sample unit number	*Remnant*	*Contiguous forest*
1	10.17	10.75
2	19.16	27.33
3	10.00	6.33
4	6.00	2.16
5	11.81	12.66
6	4.00	0.50
7	8.22	4.00
8	1.00	11.77
9	5.56	3.35
10	0.67	3.33
11	23.66	0.67
12	20.00	10.00
13	—	20.5
14	—	1.33
15	—	2.33
n	12	15
mean	10.02	7.80
SD	7.49	7.83

and probably some temporary roosting sites. But, we have no data on the use of younger redwood forests as roost sites for bats. Regardless of whether the bats were resident in the vicinity of the remnant or traveled there from elsewhere, we must still explain their significantly higher use of hollow-bearing trees in the remnant than in the unfragmented forest. We considered (1) the proximity to foraging areas, (2) the proximity to water, and (3) the density of available roost trees.

When foraging, bats often move along forest edges more than within the forest interior (Black 1974; Kunz & Martin 1982; de Jong 1994; Crampton & Barclay 1996). This may facilitate orientation but it may also maximize contact with prey (Limpens & Kapteyn 1991). The nocturnal aerial insects that are typical prey for bats are more abundant along forest edges and in recently disturbed areas than in forest interiors (Cross 1988; Grindal 1996), and bats concentrate where prey are abundant (de Jong & Ahlén 1991). Remnants with suitable roost sites may offer some bats an opportunity to minimize the distance between foraging and resting locations. Furthermore, bats may use trees in remnant stands as night roosts—between foraging bouts—and return to the contiguous forest to roost during the day. This behavior could also result in higher guano deposition rates in the remnant stands. If this were occurring we might expect that vocalizations in the remnant stands would be distributed more evenly throughout the night and that those in the contiguous stands would occur primarily at the onset of activity. The temporal pattern of bat passes, however, showed no clear differences; most activity at both stand types occurred in the hour or two immediately after sunset.

Not only were the basal hollows within the remnants closer to edge habitat that may provide diverse foraging opportunities, but they also were five times closer to the largest stream course in the study area than were hollows in the contiguous forest. After they emerge in the evening, bats usually seek open water for drinking and foraging (Christy & West 1993), and our earlier study demonstrated greater use of redwood trees that were closer to available water (Gellman & Zielinski 1996). Bats drink at open water and are also attracted to insect prey abundant in riparian areas (Cross 1988; Thomas & West 1989), two reasons to expect bats to use roosts that minimize the distance among foraging, drinking, and resting areas. *Myotis yumanensis*, in particular, is closely associated with stream courses as both feeding and drinking sites (Brigham et al. 1992).

Perhaps the most persuasive reason to expect greater use of basal hollows in the remnants is the fact that there are fewer of them per unit area than in the contiguous forest. And they occurred in a stand type—the remnant—that was itself a rare element in the landscape mosaic. The lower density of hollows within the remnant stands was probably due to isolated incidents of individual tree selection harvest and also to the inevitable increase in tree mortality and tree fall that occurs as patch size decreases (Chen & Franklin 1992). The net result was that there were fewer basal hollows available as roost sites, which may be responsible for the greater per capita use by bats. This occurred despite the fact that the mean volume of hollows in the remnant stands was substantially smaller than that in the contiguous stands, a characteristic that has previously been reported to be *negatively* associated with bat use (Gellman & Zielinski 1996). It is possible that the increased use by bats of hollows in residual stands was due to the concentration, or "packing" (Whitcomb et al. 1981; Lemkuhl et al. 1991), of individuals disturbed by timber harvest elsewhere into remaining habitat. Most of the harvest occurred 20–30 years prior to the study, however, before most of the bats could have been born, so this explanation is less likely. Despite the fact that old-growth remnants were rare in the landscape and contained fewer *and* smaller hollows than did the contiguous stands, they retained significant value to forest bats.

Our data demonstrate that small remnants of original or old-growth forest continue to function as important habitat for forest bats. This conclusion agrees with the work of Crampton and Barclay (1996), who found that *Myotis* activity levels did not change substantially following forest fragmentation, and of Fenton et al. (1992), who found that bat captures generally remained high as long as some original forest remained. Erickson and West (1996) found that *Myotis* activity was greater in mature stands, but there was no difference for a number of other species. We do not believe, however, that there is anything inherently attractive about the remnants that resulted in the increased use of basal hollows in trees that occur there. Neither is there reason to suspect that a landscape dominated by young, developing forest with a few remnants would provide better habitat for forest bats than an intact, continuous forest; substantial evidence exits to the contrary (Thomas 1988; Fenton et al. 1992; Huff et al. 1993; Krusic et al. 1996; Parker et al. 1996). The lower availability of basal hollows in the remnants and their fortuitous proximity to water probably explain why individual hollows in remnants received greater use by bats compared to those in hollows in the parkland reserve. The Wilson Creek watershed is an example of how an extremely modified landscape can continue to provide habitat for bats when most but not all of the large-cavity roosting structure has been eliminated. Our data provide an indication of the value of remnants to forest bats. The practice of harvesting the remnants to "clean up" all the miscellaneous fragments of old growth in a landscape and to bring all the stands into rotation for efficient management will probably affect bats and other wildlife. Marbled Murrelets and Northern Spotted Owls have also been reported to either nest or occur in small remnant stands of old-growth redwood (Miller & Ralph 1995; L. Diller, personal communication).

Remnants are the only old growth that occur in many watersheds. They should be viewed as the nuclei for the restoration of habitat, or at least as stepping stones in a management scheme to link larger units of forest managed for late-seral structure and function. A similar value has been recognized for small, isolated fragments of tropical forest, despite the fact that they may not be able to support all species (Turner & Corlett 1996). Remnants that are close to protected parkland, like those considered here, may actually expand the effective size of the park for species that can move easily between areas. It is apparent from the number of species associated with late-seral forest and whose habitat has been reduced by timber harvest (U.S. Forest Service & U.S. Bureau of Land Management 1994) that many species in addition to bats would benefit from protecting and linking the best of the remaining fragments of original forest.

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