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Individual legacy trees influence vertebrate wildlife diversity in commercial forests

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Abstract

Old-growth forests provide important habitat elements for many species of wildlife. These forests, however, are rare where lands are managed for timber. In commercial forests, large and old trees sometimes exist only as widely-dispersed residual or legacy trees. Legacy trees are old trees that have been spared during harvest or have survived stand-replacing natural disturbances. The value of individual legacy trees to wildlife has received little attention by land managers or researchers within the coast redwood (*Sequoia sempervirens*) region where 95% of the landscape is intensively managed for timber production. We investigated the use of individual legacy old-growth redwood trees by wildlife and compared this use to randomly selected commercially-mature trees. At each legacy/control tree pair we sampled for bats using electronic bat detectors, for small mammals using live traps, for large mammals using remote sensor cameras, and for birds using time-constrained observation surveys. Legacy old-growth trees containing basal hollows were equipped with 'guano traps'; monthly guano weight was used as an index of roosting by bats. The diversity and richness of wildlife species recorded at legacy trees was significantly greater than at control trees (Shannon index = 2.81 versus 2.32; species = 38 versus 24, respectively). The index of bat activity and the number of birds observed was significantly greater at legacy trees compared to control trees. We found no statistical differences between legacy and control trees in the numbers of small mammals captured or in the number of species photographed using remote cameras. Every basal hollow contained bat guano and genetic methods confirmed use by four species of bats. Vaux's swifts (*Chaetura vauxi*), pygmy nuthatches (*Sitta pygmaea*), violet-green swallows (*Tachycineta thalassina*), and the long-legged myotis (*Myotis volans*) reproduced in legacy trees. As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add significant habitat value to managed redwood forests. This value probably is related to the structural complexity offered by legacy trees. The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, therefore, to commercial forest stands. The results of our study call for an appreciation for particular individual trees as habitat for wildlife in managed stands. This is a spatial resolution of analysis that, heretofore, has not been expected of managers. The cumulative effects of the retention of legacy trees in commercial forest lands could yield important benefits to vertebrate wildlife that are associated with biological legacies.

Keywords: Biodiversity; Legacy tree; Biological legacy; Forest management; Managed forests; Northwestern California; Redwood; *Sequoia sempervirens*; Basal hollows; Wildlife communities; Bats; Small mammals; Birds

1. Introduction

The conservation of old-growth forests has received much attention in recent decades with the heart of the

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debate focusing on the value of old-growth as habitat for wildlife. Structural components of old-growth forests, such as snags, living trees with decay, hollows, cavities and deeply furrowed bark, provide habitat for many species (Bull et al., 1997; Laudenslayer, 2002). However, remnant old-growth trees and snags are rare in landscapes that are intensively managed for wood products. Homogenous young stands lacking structural and compositional complexity reduce the habitat value for species associated with old-growth forests (McComb et al., 1993; Carey and Harrington, 2001). The value of individual old-growth structures to wildlife in managed landscapes has received little attention by land managers or researchers (Hunter and Bond, 2001).

In some forest ecosystems, lands managed for timber production occupy all but a small portion of the landscape. In coast redwood (*Sequoia sempervirens*) forests, only 3–5% of the original old-growth redwood forest remains, largely as fragments scattered throughout a matrix of second and third-growth forests (Fox, 1996; Thornburgh et al., 2000). The remnants vary in size from large, contiguous forest patches protected in state and federal parks to patches of only a few hectares in size, to individual legacy trees in managed stands. Individual old-growth trees that have, for one reason or another been spared during harvest, or have survived stand-replacing natural disturbances, are referred to as ‘‘legacy’’ trees (Franklin, 1990). We define legacy trees as having achieved near-maximum size and age, which is significantly larger and older than the average trees on the landscape. This distinguishes them from other ‘residual’ trees, which may also have been spared from harvest but are not always larger and older than the average trees in the landscape.

The rarity of old-growth forests in managed landscapes combined with the rising economic value of old-growth redwood increases the likelihood that legacy stands and individual legacy trees will be harvested. At this time, there is no specific requirement for the retention of legacy trees during timber harvests on private or public lands in California. Exceptions occur on lands owned by companies that are certified as sustainable forest managers (Viana et al., 1996; SmartWood Program, 2000) and as such, are required to maintain and manage legacy old-growth trees.

A number of studies have demonstrated the importance of legacy and residual trees to wildlife. In Douglas-fir (*Pseudotsuga menziesii*) forests, flying squirrel abundance and nest locations were most often found in second-growth forests containing residual trees (Carey et al., 1997; Wilson and Carey, 2000). In addition, horizontal structural complexity increased in stands containing residuals (Zenner, 2000). In eastern hardwood forests, residual trees provided important habitat elements to forest birds in regenerating clear-cut stands (Rodewald and Yahner, 2000). In young and homogenous stands of regenerating redwood forests, residual old-growth legacy trees appear to be important roosting, foraging, resting, and breeding sites for spotted owls (*Strix occidentalis*), fishers (*Martes pennanti*), bats, Vaux’s swifts (*Chaetura vauxi*), and marbled murrelets (*Brachyramphus marmoratus*) (Folliard, 1993; Klug, unpublished data; Thome et al., 1999; Zielinski and Gellman, 1999; Hunter and Mazurek, in press). In the preceding studies, the value of legacy structures was identified only as a consequence of studies on the individual species of wildlife. Our goal was instead to focus our research effort on the rare habitat element itself (the legacy tree) and determine how a variety of wildlife taxa may use it, compared to commercially-mature trees in the same stand.

2. Methods

2.1. Study area

The research was conducted during 2001 and 2002 in Mendocino County, California, in the central portion of the redwood range (Sawyer et al., 2000) in the Northern California Coast ecoregion (Bailey, 1994). The study area was approximately 1750 km^2 in size and included lands owned and managed by the Mendocino Redwood Company (MRC), the California Department of Forestry and Fire Protection-Jackson State Demonstration Forest (JSDF), and Hawthorne Timber Company (HTC)/Campbell Timberland Management (Campbell). These landowners manage approximately 65% of all coast redwood timberlands in Mendocino County.

MRC lands comprise 94,089 ha of timberlands in Mendocino and Sonoma Counties and are certified as sustainable under the Forest Stewardship Council and the Smart Wood Programs (Certificate No. SW-FM/COC-128). HTC/Campbell land includes 74,264 ha of commercial redwood forest. JDSF is 20,639 ha of primarily second and third-growth redwood and Douglas-fir forests. Silvicultural prescriptions for each of the ownerships include about equal measures of even and uneven-aged harvest.

Elevations ranged from 44 to 576 m. Seasonal temperatures range from 18.2 to 9.4 °C in summer and from 13.3 to 5.5 °C in winter. Forests in this region are dominated by coast redwood. Other common trees species include Douglas-fir, grand fir (*Abies grandis*), tan oak (*Lithocarpus densiflora*), bigleaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*).

2.2. Site and tree selection

For the purposes of our research, we defined a legacy tree as any old-growth redwood tree that was >100 cm diameter at breast height (dbh) and possessed at least some of the following characteristics: deeply furrowed bark, reiterated crown, basal fire-scars, platforms, cavities, and one or more 'dead-tops'. Many legacy trees also had basal hollows ('goose pens') but absence of this trait did not exclude a tree from consideration. Legacy trees were represented by other species than coast redwood (e.g. Douglas-fir) but were not included in this study.

Thirty legacy trees were discovered using information provided by the landowners/managers and by our own reconnaissance. For a legacy tree to be selected for study the stand surrounding it must not have undergone timber operations at least 1 year prior to sampling nor could the stand have been proposed for alteration during the course of the study. The most recent harvest method varied from stand to stand but the majority of stands ($n = 27$) had been harvested under some type of selection method.

Legacy trees included those with and without basal hollows. Basal hollows occur as a result of periodic fires that produce repeated scarring and healing (Finney, 1996). To qualify as a hollow, the internal height must have been greater than the external height of the opening. Otherwise, the structure was considered a fire-scar when the cambium of the tree showed clear signs of effects from fire. We assumed that legacy trees did not need to have basal hollows to be of value to wildlife, therefore 15 legacy trees were selected that contained hollows and 15 did not.

The first step in selecting a control tree was by locating several (range = 3–10) of the largest commercially-mature trees from 50 to 100 m of a legacy tree. The set of candidates was reduced by eliminating from consideration all trees that did not share the same general environmental features with the legacy tree (i.e., similar distance to water and roads, similar slope and aspect). One control tree was randomly selected from the candidates that remained.

2.3. Wildlife sampling

2.3.1. General

An initial inspection was conducted of all trees that contained basal hollows ($n = 15$) and fire-scars ($n = 14$) by examining the interior of the hollow or fire-scar using a flashlight. These surveys were conducted during the initial portion of the study so as to not interfere with protocols designed to sample focal taxa (i.e., bats, small mammals). The hollow ceiling was searched for bats and nests of birds and mammals. The interior substrate of the hollow or fire-scar was inspected for evidence of use (e.g., feces, feathers, hair, prey remains, rest sites). Legacy and control trees were also visited regularly during the application of taxa-specific survey methods. Each time a tree was visited, field personnel would conduct an initial inspection for signs of use by wildlife.

2.3.2. Bats

We used Anabat II bat detectors (Titley Electronics, Australia) to record bat vocalizations at the trees, following the methods of Hayes and Hounihan (1994). The total number of vocalizations ('bat passes': Krusic et al., 1996; Hayes, 1997) was used to compare activity in the immediate vicinity of the legacy and control trees. To account for temporal variation in bat detections, we used a paired design and sampled simultaneously at the legacy and control trees at each site (Hayes, 1997). Bat detectors were located between 5 and 10 m from the trees, placed 1.4 m above the ground and at a 45° angle directed at the tree, a configuration that maximizes detection rates (Weller and Zabel, 2002). Each pair was sampled four times for two consecutive nights each (total = 8 nights), between either June (2002) or July (2001) and September.

Guano sampling occurred only at trees with basal hollows, using guano collection methods outlined by Gellman and Zielinski (1996). In addition to sampling guano in the 15 legacy trees with basal hollows, we also installed traps in three legacy trees with fire-scars. The oven-dried weight of guano served as a monthly index of bat use. A sample of 100 guano pellets was selected and subjected to genetic analysis to identify species. Species-specific genetic markers were developed from a 1.56 kilobase region of mitochondrial DNA spanning the majority of the 12S and 16S ribosomal RNA genes (Zinck et al., in press). We selected pellets for analysis by choosing one pellet from each tree sampled each year, and then selecting one pellet per tree sampled each season (i.e., spring and summer) until we reached 100 pellets. All trees sampled contributed at least one pellet for analysis. Eight species that occur in our study area can be identified using this method and one group of three species (*Myotis evotis*, *M. lucifugus*, and *M. thysanodes*) can be distinguished from others but not from each other (J. Zinck, pers. comm.).

2.3.3. Small mammals

We sampled non-volant mammals using live traps. Each tree selected for study was sampled using six Sherman live traps (8 cm × 9 cm × 23 cm) and two Tomahawk live traps (13 cm × 13 cm × 41 cm) placed at the base. Also, two Sherman traps and one Tomahawk trap were elevated 1.5 m and attached to the sides of the tree in an attempt to capture arboreal mammals. Traps contained seed bait and a small amount of polyester batting for insulation and bedding. We recorded the species, age, sex, reproductive status, and weight (g) of each mammal captured. A small amount of fur was clipped from the rear hindquarter (on the left if captured at the legacy tree; on the right if captured at the control) to distinguish individuals. Two, 5-day trapping sessions were conducted at each tree between June and August.

2.3.4. Time-constrained visual observation

Time-constrained observations were conducted from May to September. We observed each legacy and control tree for evidence of use or occupancy by wildlife. In 2001 we conducted one 30 min observation session in each of the three time intervals: (1) 2 h centered at dawn, (2) mid-day centered between 1100 and 1400 h, and (3) 2 h prior to sunset. In 2002, we conducted one 30 min observation session within 2 h of sunrise and sunset. All wildlife observed on, or within 5 m of the tree was recorded. Each time an animal was observed, the observer would note one occurrence (incident) per individual, the species, the amount of time spent at the tree, and the activity. Observations were categorized as perching, fly/perch, foraging, roosting, fledging, or ‘present’ (for non-avian species).

2.3.5. Remote photographic sampling

Animals present at the base of each tree were photographed using a remotely-triggered camera system (Trailmaster TM550, Trailmaster Infrared Trail Monitors, Lenexa, KS). The combination infrared and activity sensors and cameras were directed at the base of each tree from a distance of a few meters. We restricted the field of view of the sensor such that only animals directly in front of the tree base would be detected. Cameras were checked one day after installation and then approximately every 5 days for 3 weeks. Cameras operated simultaneously at each legacy and control tree in a pair. Each photo of an animal was considered a single detection, but we excluded all but one of a set of photographs of the same species taken consecutively during any 24 h period. This eliminated instances where animals would be present at the tree for several hours. We also excluded photographs of all small mammal species that were captured during the trapping sessions. All cameras operated during April–September.

2.4. Vegetation sampling

We collected physical measurements of each tree and of all basal hollows using variables described in Gellman and Zielinski (1996). We also measured vegetation attributes in the immediate vicinity of a random sample of 15 pairs of trees to determine whether the structure of the vegetation surrounding legacy and control trees differed. If such differences existed, it is possible that they would affect the use of the trees by wildlife, independent of the characteristics of the legacy and control trees themselves. We used variable-radius plot methods to estimate basal area (20-factor prism), and each tree that was included in the prism sample was also identified to species and its diameter, height, and condition was recorded. Within an 11.3 m fixed radius plot, and centered on the legacy or control tree, all logs >25.4 cm diameter were recorded by species and their length and diameter measured. Canopy, shrub, herbaceous, and ground cover (duff and downed wood) were estimated visually within a 5 m fixed radius plot.

2.5. Species diversity

We used the Shannon index (Magurran, 1988, p. 34) to characterize the diversity of species detected at legacy and control trees. Diversity indices were calculated separately for the results from the small mammal sampling, time-constrained observation surveys, remote camera surveys, and for these three survey methods combined. We used the number of individuals captured (small mammal surveys), the number of detections (camera surveys) and the number of incidents (visual observation surveys) to calculate the proportion of individuals observed for all species. Our diversity calculations for the visual observation surveys (both individual and combined with the two other surveys) excluded species that were engaged in nesting activities that included frequent forays to and from a nest site (i.e., pygmy nuthatches (*Sitta pygmaea*) and violet-green swallows (*Tachycineta thalassina*)). We also calculated species evenness, a measure of the ratio of observed diversity to maximum diversity (Pielou, 1969), for each survey type described above.

2.6. Statistical analyses

Species diversity indices were statistically compared using the methods of Hutcheson (1970), which calculates a variance for each diversity statistic then provides a method of calculating *t*-values to test for significant differences between samples (Magurran, 1988, p. 35). Small mammal trapping, time-constrained observation and remote photograph (medium and large mammals only) data were analyzed using matched-pair *t*-tests. We were unable to normalize the results of the camera (all animals) data and thus used a non-parametric signed-rank test (*S*) to compare the number of detections by photograph at legacy and control trees. We used a mixed-effects analysis of variance model to compare bat detections between legacy and control trees.

Vegetation characteristics in the immediate vicinity of the legacy and control tree were compared using either *t*-tests (continuous variables) or χ^2-tests (categorical variables). All statistical analyses were conducted using SAS, Version 8.2 (SAS Institute, 2001, Cary, NC). Statistical significance was implied if P was <0.05.

3. Results

As expected, legacy trees were larger in diameter (mean dbh = 293 cm (S.D. = 82.3)) and height (mean = 53 m (S.D. = 14.8)) than the control trees (mean dbh = 73 cm (S.D. = 15.2), mean height = 32 m (S.D. = 10.2)). However, the mean diameter of control trees was 72.5 cm dbh, which is considered a commercially-mature size (R. Shively, pers. comm., 2001, Mendocino Redwood Company).

3.1. General wildlife observations

Initial examinations of the trees indicated that most of the hollows and fire-scars in legacy trees ($n = 19$; 63%) had evidence of small mammal use on the basis of the discovery of feces, food remains, or nest evidence (usually dusky-footed wood rat *Neotoma fuscipes* middens, $n = 5$). One hollow contained four roosting bats and six hollows (40%) contained guano, evidence of bat use. Four hollows or fire-scarred legacy trees (13%) had evidence of use (i.e., claw marks) by large mammals and feces or nests indicated that 10 legacy trees (33%) were used by birds.

The general inspection of trees resulted in several noteworthy observations of reproductive activity:

(1) On 16 June 2002, two adult pygmy nuthatches were observed repeatedly entering and exiting a cavity in a legacy tree. The birds were observed entering the cavity with food, which was followed by vocalizations of young.
(2) A legacy tree contained a large cavity that was occupied by barn owls (*Tyto alba*) during both years of the study. Fresh feces and food pellets were observed during each visit to the tree.
(3) On 16 July 2002, violet-green swallows were observed repeatedly entering and exiting a cavity in a legacy tree. These behaviors, and the time of

year, suggest the birds were nesting within the cavity.

(4) Vaux's swifts nested for two consecutive years in the basal hollow of a legacy tree.

(5) On 23 July 2002 a large number of bats was observed in a hollow that had conspicuous guano accumulation and in which was discovered, on 31 July 2001, a dead juvenile long-legged myotis. Collectively, this evidence suggests that this legacy tree was used as a maternity colony.

3.2. Bats

3.2.1. Acoustic sampling

We recorded a total of 10,799 bat passes over the two sample years. The mean index of bat activity was significantly greater at the legacy trees compared to the control trees ($F_{1,45.7} = 17.66, P < 0.0001$) (Fig. 1). The mean index of bat activity at legacy trees with and without hollows was 34.8 (S.D. = 33.4, $n = 15$) and 22.6 (S.D. = 15.9, $n = 15$), respectively, a difference that was not statistically significant ($t = 1.27$, $P = 0.21$).

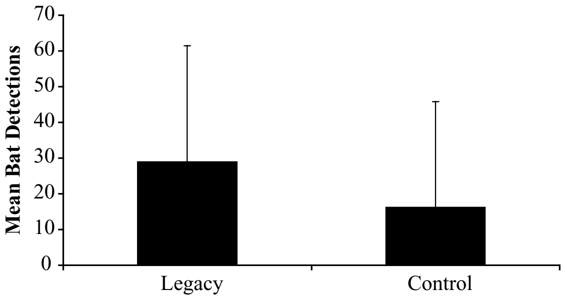

Fig. 1. Mean bat detections and standard deviation for legacy and control trees ($F_{1,45.7} = 17.66$, $P < 0.0001$) in Mendocino County, California, 2001 and 2002.

3.2.2. Guano sampling

We collected guano monthly from July to October 2001 and April to October 2002. All hollows and fire-scars showed evidence of bat use during some portion of the survey period. Average guano weight declined from August to October during both years (Fig. 2).

Sixty-eight of the 100 guano samples submitted for analysis amplified adequate amounts of DNA for species analysis. Four species were verified to use legacy trees, with the long-legged myotis the most common (46%) (Table 1). The California myotis (*Myotis californicus*) was the species detected at the greatest number of hollow-bearing trees (73%) and the total number of trees (hollow-bearing and fire-scarred (66%)). The big brown bat (*Eptesicus fuscus*) and the California myotis were the only species identified from the four guano samples that originated from fire-scars (Table 1).

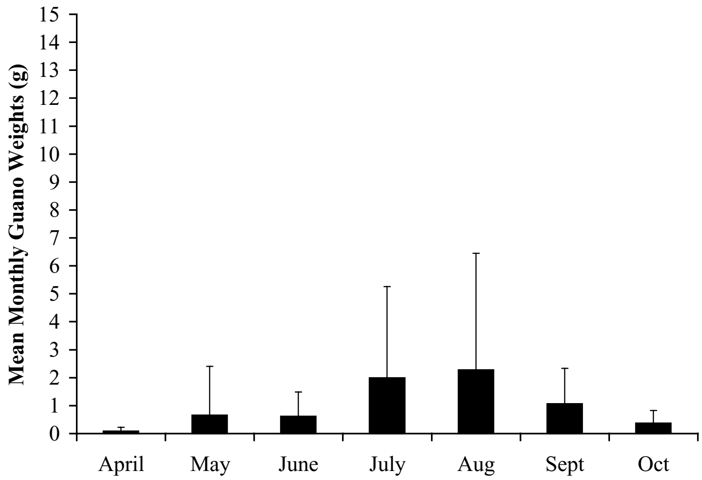

Fig. 2. Mean monthly guano weights (g) and standard deviation (April–October) at 14 hollow-bearing trees in Mendocino County, California, 2001 and 2002.

Table 1
Number of 68 guano samples collected from 15 basal hollows and three fire-scars that could be identified to species

Species	Guano sample		Hollows		Fire-scars		Trees total	
	Number	Percentage of samples	Number	Percentage of hollows	Number	Percentage of fire-scars	Number	Percentage of trees total
Big brown bat (*E. fuscus*)	9	13	5	33	3	100	8	44
California myotis (*M. californicus*)	17	25	11	73	1	33	12	66
Myotis 3[a]	11	16	5	33	0	0	5	27
Long-legged myotis (*Myotis volans*)	31	46	9	60	0	0	9	50

[a] *Myotis lucifugus*, *M. evotis*, and *M. thysanodes* are not currently distinguishable, but guano from these three species can be distinguished from other species.

3.3. Small mammal sampling

There was a slightly greater number of total small mammal captures at legacy trees compared to control trees (Table 2). There was also a greater number of individuals captured at the legacy trees compared to control trees, though this relationship was not statistically different ($t = 0.5$, $P = 0.62$). Two of the insectivores (shrew mole (*Neurotrichus gibbsi*) and Trowbridge's shrew (*Sorex trowbridgii*)) were the only species of small mammals that appeared to be trapped more commonly at the base of legacy trees.

3.4. Observation surveys

Each legacy and control tree was sampled at least twice, resulting in a total of 132 surveys and 114.5 h of survey effort (Table 3). There was a significantly greater number of incidents ($t = 16.6$, $P < 0.0001$) and time spent ($t = 4.05$, $P = 0.0004$) at legacy trees compared to control trees (Table 3). Wildlife (primarily birds) was observed about nine times as frequently at legacy trees compared to control trees and there were also more species observed at legacy trees compared to control trees (Table 4).

Of the activities observed, 82% was either perching or flying. There was twice as much foraging activity at legacy trees (22 incidents) compared to control trees (10 incidents). Woodpeckers, nuthatches, and some swallows were observed only at legacy trees; acorn woodpeckers used a legacy tree as a food storage location (i.e., granary). The majority of individuals observed were pygmy nuthatches, violet-green swallows, or unknown passerines.

Remote cameras operated a total of 1278 survey hours. We photographed 18 species at legacy and control trees; 13 species were detected only as a result of the camera surveys (Table 5). The total number of photographic detections was 38 at legacy trees (mean = 1.4, S.D. = 2.4, $n = 27$) and 17 at control

Table 2
Summary of small mammal captures by species at study sites in Mendocino County, California, 2001 and 2002

Species	Total captures		Total individuals captured		Individuals captured at both legacy and control pair
	Legacy	Control	Legacy	Control	
Trowbridge's shrew (*S. trowbridgii*)	33	18	30	16	0
Fog shrew (*S. sonomae*)	2	4	2	3	0
Shrew mole (*N. gibbsii*)	5	0	5	0	0
Short-tailed weasel (*Mustela erminea*)	0	1	0	1	0
Dusky-footed wood rat (*N. fuscipes*)	62	88	23	37	0
Redwood (yellow-cheeked) chipmunk (*Tamias ochrogenys*)	93	51	39	31	3
Deer mouse (*Peromyscus maniculatus*)	150	133	67	61	1
Western red-backed vole (*Clethrionomys californicus*)	20	37	13	19	0
Total	365	332	179	168	4

Table 3
Summary of visual observation results[a]

Tree type	Total			Survey period					
	Total survey effort (h)	min/h	Number of incidents	a.m.		Mid		p.m.	
				min/h	Number of incidents	min/h	Number of incidents	min/h	Number of incidents
Legacy	57.5	0.0998	188	0.1035	170	0.002	4	0.1938	14
Control	57.0	0.0105	34	0.0143	27	0.003	6	0.0024	1

[a] Total survey effort, duration (min/h of survey effort) that individuals were observed and the total number of incidents of wildlife observed for three time periods; a.m. (within 2 h of sunrise), mid (2 h centered around mid-day) and p.m. (2 h within sunset).

trees (mean = 0.63, S.D. = 1.3, $n = 27$); the means were not statistically different ($S = 37.5$, $P = 0.10$). When we restricted detections to include only medium and large mammals the total numbers of detections were 14 (mean = 0.52, S.D. = 0.64) and 10 (mean = 0.37, S.D. = 0.88) at legacy and control trees respectively, but were not statistically different ($t = 0.78$, $P = 0.44$).

Table 4
Species observed at legacy and control trees and the number of incidents (number of times a species was observed) during time-constrained visual observations in Mendocino County, California, 2001 and 2002

	Legacy	Control
Species at legacy only		
Acorn woodpecker	12	0
Common raven	2	0
Downy woodpecker	1	0
Hairy woodpecker	3	0
Northern flicker	2	0
Osprey	1	0
Pygmy nuthatch	25	0
Red-breasted nuthatch	1	0
Turkey vulture	1	0
Unknown flycatcher	1	0
Unknown owl	1	0
Unknown swallow	11	0
Unknown woodpecker	4	0
Vaux's swift	3	0
Violet-green swallow	52	0
Winter wren	2	0
Species at control only		
Golden-crowned kinglet	0	1
Hutton's vireo	0	8
Species at both legacy and control		
Brown creeper	4	2
Chestnut-backed chickadee	4	2
Hermit warbler	1	1
Pacific-slope flycatcher	1	1
Redwood chipmunk	1	1
Steller's jay	10	7
Unknown passerine	44	10
Western gray squirrel	1	1

3.5. Vegetation sampling

There were no differences in the vegetation characteristics in the area immediately surrounding the legacy and control trees. Basal areas, tree diameters, tree heights, log volumes, canopy cover, shrub cover, and herbaceous cover were statistically indistinguishable (Table 6). In addition, there were no significant

Table 5
List of species and the number of detections (photographs) at legacy and control trees during remote camera surveys in Mendocino, California, 2002[a]

	Legacy	Control
Species at legacy only		
Bat (species unknown)	1	0
Brush rabbit (*Sylvilagus bachmani*)	7	0
Sonoma vole (*Arborimus pomo*)	1	0
Winter wren (*Troglodytes troglodytes*)	1	0
Species at control only		
Gray fox (*Urocyon cinereoargenteus*)	0	2
Raccoon (*Procyon lotor*)	0	1
Species at legacy and control		
Black bear (*Ursus americanus*)	4	1
Black-tailed deer (*Odocoileus hemionus*)	1	1
Bobcat (*Lynx rufus*)	4	1
Douglas' squirrel (*Tamiasciurus douglasii*)	5	4
Spotted skunk (*Spilogale gracilis*)	1	1
Striped skunk (*Mephitis mephitis*)	4	3
Western gray squirrel (*Sciurus griseus*)	9	3

[a] Each detection represents only one photo per species per tree per 24 h period.

Table 6
Means and standard deviations (S.D.) for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic	Tree type				t	P
	L		C			
	Mean	S.D.	Mean	S.D.		
Basal area (m^2/ha)	55.6	22.5	56.8	27.5	0.17	0.87
Tree dbh (cm)	46.7	23.2	49.2	23.6	0.38	0.71
Tree height (m)	24.6	7.7	26.2	8.3	0.87	0.40
Log volume (m^2)	1.27	1.4	0.79	0.86	1.08	0.30
Canopy cover (%)	83.6	7.6	84.4	8.2	0.42	0.68
Shrub cover (%)	12.8	16.5	16.1	21.2	0.63	0.54
Herbaceous cover (%)	24.9	36.8	16.7	23.6	1.19	0.30

[a] Legacy and control trees were excluded from calculations. t-values and P-values are from the results of matched-pair t-tests.

differences in tree species, tree condition, log species, log condition, the amount of duff, or the amount of downed wood (Table 7). Thus, we concluded that there were no systematic differences in the physiognomy of vegetation surrounding legacy trees when compared to control trees.

3.6. Diversity indices

The number and diversity of species using legacy trees was greater than those using control trees using data from only the time-constrained observation surveys, or when we combined the results from the time-constrained observation surveys, camera surveys, and small mammal trapping (Table 8). Species richness was about 1.5 times as great at legacy trees ($n = 38$) than at control trees ($n = 24$) for all surveys. Using data from the timed observation surveys only, the species richness was more than twice as great at legacy

Table 7
Frequency of occurrence for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic		Frequency for tree type		χ^2	P
		L	C		
Tree species	Coast redwood	22	22	2.03	0.36
	Other conifer	15	12		
	Hardwood	20	10		
Tree condition	Live	40	33	2.42	0.3
	Declining	13	5		
	Dead	4	5		
Log species	Coast redwood	31	27	0.63	0.73
	Other conifer	10	9		
	Hardwood	4	6		
Log condition	Class 1	2	1	1.05	0.9
	Class 2	8	8		
	Class 3	15	11		
	Class 4	13	12		
	Class 5	7	9		
Downed wood	High	7	8	0.13	0.72
	Low	8	7		
Duff	High	13	12	NA	NA
	Low	2	3		

[a] Legacy and control trees were excluded from calculations. Statistical values are from χ^2 goodness of fit tests.

Table 8
Number of individuals (small mammals) or detections (other taxa), species richness, evenness and diversity indices by survey method for legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Survey method	Tree type	Number of individuals or detections	Richness (number of species)	Evenness	Shannon diversity index	t statistic	d.f.	P
Observation	L	111	22	0.73	2.25	2.13	95	0.05–0.02
	C	34	10	0.82	1.88			
Trailmaster	L	38	11	0.88	2.11	0.64	54	>0.5
	C	17	9	0.93	2.04			
Mammal trapping	L	179	7	0.82	1.60	0.26	350	>0.25
	C	168	7	0.82	1.58			
Overall	L	328	38	0.77	2.81	5.05	481	<0.001
	C	219	24	0.73	2.32			

[a] Tests statistics refer to the Shannon diversity indices.

trees ($n = 22$) than at control trees ($n = 10$). The Shannon diversity indices were statistically higher at legacy trees (2.81) than control trees (2.32) for the combined surveys and for the observational surveys (human observer) (Table 8), but we did not find differences in the richness or diversity of small mammals captured in traps or for the species detected by cameras, when these data sets were analyzed separately (Table 8). Evenness was greater at legacy trees compared to control trees for the combined surveys only (Table 8).

4. Discussion

As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add important foraging and breeding habitat value to redwood forests managed for timber. The use of legacy trees by wildlife was demonstrated by evidence of their nesting, roosting and resting; behaviors which were not observed at control trees. This difference is probably related to the structural complexity offered by redwood legacy trees (Bull et al., 1997; Laudenslayer, 2002). Control trees were smooth-boled with very few large horizontal limbs, few cavities, and no basal hollows. Legacy trees possess these structural features, which probably account for their greater attractiveness to a variety of wildlife species.

The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, as a result, to commercial forest stands. However, we did not sample specifically for wildlife that may benefit from the presence of large horizontal branches (e.g. platform nesting wildlife). Basal hollows were used by every taxa sampled, but appear to be particularly important to bats and birds. In addition to the fact that guano was collected at every hollow we sampled, individual bats were observed in hollows, and reproduction was documented. Use of basal hollows by bats has been observed in other redwood regions (Gellman and Zielinski, 1996; Zielinski and Gellman, 1999; Purdy, 2002) and there are several previous reports of basal hollows used by bats for reproduction (Rainey et al., 1992; Mazurek, in press). Hollows also appear to be important nest sites for some bird species, in particular Vaux's swifts (Hunter and Mazurek, in press). Because roost and nest availability can limit the populations of birds and bats (Humphrey, 1975; Kunz, 1982; Brawn and Balda, 1988; Christy and West, 1993; Raphael and White, 1984), basal hollows may play a critical role in the redwood region if they provide roost and nest sites in forests that are otherwise deficient. The increased use of legacy trees by insectivorous birds and bats may also be because the rugosity of the bark may harbor a greater diversity and abundance of insects (Ozanne et al., 2000; Willett, 2001; Summerville and Crist, 2002). Bark gleaners, such as brown creepers (*Certhia americana*), have been correlated with the abundance of spiders and other soft-bodied arthropods that are significantly associated with bark furrow depth (Mariani and Manuwal, 1990); this may also explain the disproportionate use of legacy trees by nuthatches and woodpeckers. Finally, basal hollows not only benefit the wildlife that use them but the trees in which they are found. The feces of animals that are attracted to hollows can be an important source of nutrients for trees that may be on nutrient-poor sites (Kunz, 1982; Rainey et al., 1992).

The mammal data (bats excluded) did not suggest a disproportionate association with either legacy or control trees. Possible exceptions include two insectivores, which were captured more at legacy trees, and the dusky-footed woodrat, whose nests were found in five of 15 basal hollows. Shrew moles are associated with older forests (Raphael, 1988; Carey and Johnson, 1995) and are infrequently found in logged areas (Tevis, 1956). Several studies also found that Trowbridge's shrews have a similar association with mature forest conditions (Gashwiler, 1970; Hooven and Black, 1976; Carey and Johnson, 1995).

The camera data did not reveal disproportionate use of legacy trees by mammals. Relatively few mammalian carnivores were detected at either type of tree, perhaps because some species (i.e., the marten (*Martes americana*) and the fisher (*M. pennanti*)) are sensitive to forest habitat loss and fragmentation (Buskirk and Powell, 1994) and have been either extirpated from the region or are very rare (Zielinski et al., 1995, 2001). With the exception of the two insectivores and wood rats, none of the non-volant mammals we sampled appeared to be strongly associated with the legacy trees. Unlike the passerine birds, which use the structurally complex bark of legacy trees for foraging and cavities for nesting, and the bats, which roost in hollows and bark crevices, our data do not indicate that legacy trees have exceptional value for rodents or for the species of carnivorous mammals that still occur in the region.

Our conclusions about the value of legacy trees to wildlife in the redwood region are supported by the results of studies on individual species of wildlife elsewhere. Legacy trees (also described as old-growth residuals) are used by northern (*Strix occidentalis caurina*) and California (*S. o. occidentalis*) spotted owls for nesting and roosting (Moen and Gutiérrez, 1997; Irwin et al., 2000). Fishers use legacy conifers, and residual hardwoods, as daily rest sites in public Douglas-fir forests (Seglund, 1995) and private redwood forests (R. Klug, pers. comm.). Flying squirrels were twice as abundant when legacy trees were retained in managed areas (Carey, 2000) and their diet was found to be more diverse in legacy stands (Carey et al., 2002).

Our work was directed at assessing the value of individual *legacy* trees in stands, but there is a considerable body of research on the related question of what value *residual* trees and patches have in maintaining wildlife diversity in forests. Residual structures may not be as old as the legacy structures we studied, but they can add important structural diversity to which many species of wildlife respond. Songbirds in a variety of coniferous mixed, and hardwood forest types have benefited from the retention of residual trees (Hobson and Schieck, 1999; Rodewald and Yahner, 2000; Schieck et al., 2000; Tittler et al., 2001; Whittman et al., 2002; Zimmerman, 2002). Southern red-backed voles (*Clethrionomys gapperi*), a late-successional associated forest species, are also more common in harvested areas as the basal area in residual trees increases (Sullivan and Sullivan, 2001). The retention of residual structure during logging appears to have benefits to wildlife, but additional research will be necessary to distinguish the effects of retaining commercially mature—but relatively young—trees for wildlife from retaining and managing legacy trees, which are typically much older.

The goal of this study was to document the pattern and frequency of use of legacy and control trees so that we might better understand how young and old elements are used within the matrix of commercial redwood forests. To do so we compared the occurrence of species and individuals, but did not evaluate how individual trees contribute to *survival* or *reproduction* (i.e., fitness) of individual species. Measures of abundance, or indices of abundance, are not sufficient to completely evaluate the effects of variation in habitat on wildlife populations; in some cases they can even mislead because not all places where animals occur are suitable for reproduction (Van Horne, 1983). Our observations of reproductive behavior by a number of birds and at least one species of bat, however, suggest that legacy trees may influence the fitness of some species as well. We also believe that the potential survival value of access to legacies was probably underestimated in our study because we evaluated use only during the climatically benign summer months. We expect that benefits of access to legacy trees would be the greatest during the winter when they would be used as refuges from inclement weather (e.g., Carey, 1989).

If legacy trees provide one of the few choices for nesting and reproductive sites, and they are rare, then it is possible that they may be easily located and searched by predators making them population ‘sinks’ (Pulliam, 1988). Tittler and Hannon (2000) did not find increased predation in this respect, but their study evaluated residual trees, which were more numerous and probably not as distinctive and obvious foraging locations as are the more structurally distinctive redwood legacy trees. It is clear, however, that the risks that wildlife may be subjected to when using, and perhaps congregating at, legacy structures will need to be evaluated with respect to the benefits.

5. Conclusions

Our traditional view of conservation reserves is of large protected areas. However, few landscapes provide us with the opportunity to preserve large tracts of land and we must consider conserving biodiversity within the matrix of multiple use lands (Lindenmayer and Franklin, 1997). Given the fragmented nature of mature forests in the redwood region, remnant patches of old-growth and individual legacy trees may function as ‘mini-reserves’ that promote species conservation and ecosystem function. Legacy structures increase structural complexity in harvested stands and, as a result, can provide the 'lifeboats' for species to re-establish in regenerating stands (Franklin et al., 2000). Although the lifeboat function may not be entirely fulfilled for vertebrates with large area needs, these habitat elements may make it possible for some species to: (1) breed in forest types where they may otherwise be unable, and (2) secure a greater number of important refuges from climatic extremes and predators. In addition, these functions may allow legacy trees to provide some measure of habitat connectivity ('stepping stones') to larger more contiguous tracts of old-growth forests (Tittler and Hannon, 2000; Noss et al., 2000).

Because of their rarity in commercial forests, the first step in the management of legacy trees is to determine their locations and protect them from logging or from physical degradation of the site. Because legacy redwoods with basal hollows are even more rare, locating and protecting these should be the highest priority. In addition, the circumstances that lead to their genesis will be difficult to recreate, especially on commercial timberland. Hollows form by repeated exposure of the base of trees to fire (Finney, 1996), and because most fires on private land are suppressed, prescribed fire would need to be repeatedly applied to trees that would be designated as 'future legacies' and which would be excluded from harvest in perpetuity. We hasten to add, however, that legacy trees without basal hollows appear to have significant benefits to wildlife. Even without management to encourage basal hollows we suggest that managers plan for the recruitment of trees that are destined to become legacies. This will require their protection over multiple cutting cycles. We expect that new silvicultural methods will be required to prescribe the process of identifying, culturing, and protecting residual legacy trees. Although we do not believe that any one tree will protect a species, we do believe that the cumulative effects of the retention, and recruitment, of legacy and residual trees in commercial forest lands will yield important benefits to vertebrate wildlife and other species of plants and animals that are associated with biological legacies.

The results of our study beg us to consider habitat at a spatial scale that is smaller than that of habitat patches or remnant stands; we conclude that *individual trees* can have very important values to wildlife. More research would be helpful, however, to specify the level of individual tree retention required to maintain biodiversity in managed lands (Lindenmayer and Franklin, 1997). It would help to know, for example, whether the fitness of individual species, and the diversity of wildlife communities, is greater in landscapes in which legacy trees are common compared to landscapes with very few legacy trees. It is possible that because legacy trees are rare—despite their apparent values to wildlife—that they do not affect wildlife diversity or productivity over large areas. It would also advance our knowledge to determine whether legacy trees in legacy-rich landscapes can function to maintain connectivity between protected stands of mature and old-growth forests. If so, the landscape context will be an important component of managing residual legacy trees and planning their recruitment across landscapes. For now, however, this study makes clear that protecting legacy trees will protect important habitat features that receive disproportionate use by many wildlife species. The protection and management of these trees can enhance wildlife conservation on lands where the opportunities to do so can be limited.

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