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BAT ACTIVITY ALONG INTERMITTENT STREAMS IN NORTHWESTERN CALIFORNIA

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Bats are known to use areas above perennial streams and rivers for foraging and traveling; however, little is known about bat use of smaller streams that flow intermittently. We compared bat activity among 3 size classes of streams and upland sites in a northwestern California watershed during summers 1996 and 1997. Stream size was classified based on channel width. Ultrasonic Anabat II® bat detectors were placed in stream channels and at upland sites, and bat activity was recorded remotely at night. Analysis of bat detector data revealed a significant difference in activity among the 4 habitat types in both years. In 1996, bat activity was greatest along medium and large intermittent streams, was intermediate at small intermittent streams, and was least at upland sites. In 1997, a similar pattern was found, but no significant difference was found in bat activity between small stream and upland sites. To determine species presence, bats were captured in mist nets at stream sites with the highest bat activity. Results are presented indicating differences in number of captures by species between medium and large streams.

Key words: bat activity, bat detectors, California, Douglas fir, intermittent streams, mistnetting

Current guidelines for management of federal lands in the Pacific Northwest are dictated by the Record of Decision that followed the Northwest Forest Plan (United States Department of Agriculture and United States Department of Interior 1994). The Record of Decision requires that intermittent streams (nonpermanently flowing streams that have a definable channel with signs of annual scour and deposition) have a buffered zone with limited management activities that has the width of 1 site-potential tree height (the average maximum height for a 200-year-old tree, at those site conditions) or a slope distance of 100 feet (33 m), whichever is greater. When this plan was being developed, bats were identified as an important group of species in justifying riparian protection. Although bat use of permanent streams, ponds, and lakes is well established, very little is known regarding use of intermittent streams by bats.

Riparian areas are important foraging habitats for bats (Brigham et al. 1992; Cross 1986; Furlonger et al. 1987; Grindal 1995; Thomas and West 1991). In Douglas-fir (*Pseudotsuga menziesii*) forests of the Washington Cascades and the Oregon Coast Range in the Pacific Northwest, foraging activity of *Myotis* species was 10 times greater over water than within the forest interior (Thomas 1988). In coastal British Columbia, the little brown bat (*M. lucifugus*) was 75 times more active over lakes and ponds than in forested habitat (Lunde and Harestad 1986). In the Washington Cascades, greater abundances of small- and medium-sized insects were found in ripari

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an than in forested habitats, and that was correlated with higher feeding rates of bats (Thomas 1988).

Bats use riparian areas for drinking and foraging. Because bats drink from water holes while flying, the pool size needed varies with flight behavior. Highly maneuverable bats, such as small species of *Myotis,* can drink from a pool a few centimeters in diameter, whereas less maneuverable, but faster fliers, such as Brazilian free-tailed bats (*Tadarida brasiliensis*) require larger pools (Cross 1986). Riparian areas also may provide roost sites for bats (Betts 1998; Cross 1988; Ormsbee and McComb 1998; Rabe et al. 1998; Tidemann and Flavel 1987). Larger, older trees commonly are selected by bats for day and night roosts (Barbour and Davis 1969; Betts 1998; Cross 1988; Ormsbee and McComb 1998; Perkins and Cross 1988; Rabe et al. 1998; Tidemann and Flavel 1987).

Our primary objective was to compare bat activity among different size classes of streams and upland sites. Our null hypothesis was that no differences would be found in bat activity among these different habitats. A secondary objective was to determine species of bats present within the study area.

STUDY AREA

We conducted our study in the Pilot Creek watershed on the Six Rivers National Forest (elevation 1,100-1,320 m) in the northern Coast Range of northwestern California (40°39'N, 123°36'W). Riparian reserves comprised about 60% of the watershed (United States Department of Agriculture, Forest Service 1994). The Pilot Creek watershed, draining about 100 km^2, was located 55 km E of the Pacific Ocean. Summers were warm and dry with an average of 4 cm of precipitation in June, July, and August. Average annual precipitation was 200 cm (United States Department of Agriculture, Forest Service 1994). Yearly precipitation at Mad River Ranger Station (elevation 846 m), located 20 km from Pilot Creek, was 253.5 cm in 1996 and 154.5 cm in 1997. During June through August at the Mad River Ranger Station, 1.3 cm and 6.1 cm of rain were recorded in 1996 and 1997, respectively. Nightly temperatures were recorded at study sites in the Pilot Creek watershed using maximum-minimum thermometers during bat-detector sampling. Mean minimum temperature was 14.5°C in 1996 and 11.3°C in 1997. Mean maximum temperature was 27.5°C in 1996 and 23.1°C in 1997.

In 1994, 60% of the Pilot Creek watershed was classified as late-successional forest, 17% of which was considered old growth (United States Department of Agriculture, Forest Service 1994). The dominant tree species in our study area was Douglas-fir but other common trees included white fir (*Abies concolor*), white oak (*Quercus garryana*), black oak (*Q. kelloggii*), canyon live oak (*Q. chrysolepis*), incense cedar (*Calocedrus decurrens*), white alder (*Alnus rhombifolia*), Pacific yew (*Taxus brevifolia*), and madrone (*Arbutus menziesii*). All sampling sites were underlain by Franciscan formation sedimentary rock. Small intermittent streams were a prevalent part of the landscape.

MATERIALS AND METHODS

Sampling was conducted from 10 June to 22 August 1996 and from 2 June to 5 September 1997. Intermittent stream size was classified based on channel width and percent water. In a related study, Waters et al. (2001) measured active channel width at 42 stream sites within the Pilot Creek watershed. From those 42 sites, we selected 4 sites within each of 3 size classes: small intermittent stream sites had a mean channel width of 0.8 m ± 0.3 SE (range = 0.1-1.2 m), medium intermittent stream sites had a mean channel width of 1.9 ± 0.0 m (1.8-2.0 m), and large intermittent stream sites had a mean channel width of 7.0 ± 1.2 m (5.5-10.5 m). Percent water was measured at each site once per month in 1996 from May through September for stream characterization purposes. Stream sites were located ≥ 125 m from another stream channel. Four upland sites were chosen based on proximity to stream sites to facilitate field logistics. Upland sites were located ≥100 m from any channel and had no standing water present in any form.

Bat activity was sampled remotely using Anabat II® ultrasonic bat detectors (Titley Electronics, Ballina, New South Wales, Australia) in conjunction with a delay switch and tape recorder (Radioshack minisette 20, model 14-1055B, Radioshack, Fort Worth, Texas)-Hayes and Hounihan 1994). Bat detectors were set to a sensitivity of 8 and a division ratio of 16, and started manually before sunset. Each sampling night, 4 different sites were sampled (1 of each stream size class and 1 upland site) with 1 bat detector at each site. Bat calls were recorded onto 120-min audio cassettes, collecting 60 min of voice-activated ultrasonic detections per site. Audio output was later used to count number of bat passes and record time of activity. We defined a bat pass as an echolocation call containing ≥2 orientation clicks (Fenton 1970; Hayes 1997; Kalcounis et al. 1999; Krusic et al. 1996; Thomas 1988; Thomas and West 1989; Walsh and Mayle 1991). A single bat pass was separated by either a calibration tone from the bat detector device or silence of ≥1 s. When multiple calls were recorded simultaneously, they were counted as 1 bat pass. No attempt was made to distinguish feeding buzzes because auditory recognition of feeding behavior may be unreliable (Weller et al. 1998).

Bat detectors provide a relative measure of bat activity (Fenton 1970; Fenton et al. 1973; Thomas 1988; Thomas and LaVal 1988). An individual bat may have been recorded more than once in or among habitats. We used bat detectors to compare the relative amounts of bat activity across habitats, not as an absolute count of individual bats using a particular site. We assumed bat-detector biases were similar for all locations. Because bat activity is greatest during the first 3 h after sunset (Jones et al. 1996; Kunz 1974; Kunz and Brock 1975; Taylor and O'Neill 1988; Thomas and West 1991; Zielinski and Gellman 1999), we recorded the number of bat passes per hour during that period to compare bat activity among habitat types. That method allowed us to use the largest data set for analyses because tapes often filled or detectors malfunctioned before the end of the night, resulting in missing data later in the night. Data collected on nights when bat detectors were deployed after sunset or did not function for ≥3 h after sunset were omitted from analyses (n = 30 detector nights).

To maximize reception of bat echolocation calls, detectors were oriented along stream axes and positioned along stream segments that had no bends or vegetation obstruction. Detectors were placed in stream channels either on the ground or on rocks and angled upward about 30°. Detectors were placed near calm pools at medium and large stream sites because bats select calm water over turbulent water for foraging and drinking (Mackey and Barclay 1989). At upland sites, detectors were placed on downed logs, angled about 30°, and oriented toward an open area. Four bat detectors were rotated systematically among sites throughout the study to account for any variation among detectors. We assumed that vocalizing bats within about 30 m of the detector would be detected based on field tests in which a 40-kHz frequency was emitted from an electronic tape measure (Sonan 60 pro model 10065, Scarsdale, New York), and the distance to the bat detector was measured.

Within a location, large differences in bat activity between consecutive nights have been found, indicating significant temporal variation in bat activity (Hayes 1997; Hayes et al. 1995). Therefore, we used a blocked design that sampled 1 site in each habitat category each night, resulting in 4 blocks. Sites within blocks were grouped spatially to simplify field logistics. Each block was sampled for 2 consecutive nights every other week throughout each field season.

Analysis of variance (general linear model) was used to test for differences in mean number of bat passes per hour among habitats, among sampling periods, and among blocks nested within habitats. We tested for differences among habitats using Tukey's post-hoc multiple comparison test. All variables were fixed in both analyses. Data were log transformed, ln(bat passes per hour + 1), to meet statistical assumptions of normality and homoscedasticity; the latter was difficult to test because data were missing. Minitab (1998) was used for all analyses. All variances are reported as mean ± 1 *SE*.

Bats were captured in mist nets to determine species present in our study area. Sex, age class, and reproductive status of individuals also were recorded. Age class was determined by degree of finger-bone epiphyseal fusion (Anthony 1988). Female abdomens were palpated for evidence of pregnancy, and mammary glands were

TABLE 1.--Means and standard errors of number of bat passes per hour during the first 3 h after sunset among habitats by year in the Pilot Creek study area, Six Rivers National Forest, California.

	1996		1997	
Habitat	$\overline{X}$ bat passes ± *SE*	Number of nights	$\overline{X}$ bat passes ± *SE*	Number of nights
Upland	3.4 ± 0.2	18	3.6 ± 0.3	32
Small stream	7.2 ± 0.3	36	4.0 ± 0.3	33
Medium stream	24.5 ± 0.3	32	27.5 ± 0.3	34
Large stream	35.6 ± 0.2	29	15.9 ± 0.2	42
Total	70.7 ± 1.0	115	51.1 ± 1.1	141

palpated to detect presence of milk (Racey 1988). Mist-net sampling occurred at 1 stream site/night. Mist-net locations were the same as bat detector locations; however, we did not use mist nets at stream sites when bat detectors were in place. Mist nets were set at stream sites where bat detectors indicated the highest bat activity. At least 10 days were allowed to pass before any given stream site was netted again. To focus our efforts on obtaining species presence data, stream sites with no captures and low bat activity were not netted again. Avinet® (Dryden, New York) 36-mm gauge mist nets were set perpendicular to channels (Cross 1986); number of nets (typically 3-4) and exact configuration were dependent upon channel morphology. Mist nets were left open for about 3 h after sunset, depending on bat activity, because that period is usually the most productive for capturing bats (Cross 1986; Jones et al. 1996; Kunz and Brock 1975; Taylor and O'Neill 1988). Bats were marked with a small dot of correction fluid (Wite-out, BIC Corporation, Milford, Connecticut) on the underside of the wing membrane to identify individuals recaptured on the same night.

RESULTS

Small, medium, and large intermittent stream sites and upland sites were sampled 69, 66, 74, and 48 nights, respectively. Sampling effort differed among habitat categories because equipment malfunctioned at irregular rates and upland sites were added midway through the field season in 1996 to allow comparison of bat activity between stream channels and upland locations. Surface water was rarely present at small stream sites; water was present only at peak snowmelt and after very large precipitation events. In 1996, mean percent water at small stream sites was 1.0 ± 1.0. Medium stream sites had surface flow that was discontinuous and sections of dry channel separated sections that had surface flow. In 1996, mean percent water at medium stream sites was 42.6 ± 5.5. At large stream sites, surface water was present throughout the year. In 1996, mean percent water at large stream sites was 96.3 ± 2.2.

Overall, mean bat activity was significantly higher in 1996 (70.7 passes/h ± 1.0 *SE*) than in 1997 (51.1 ± 1.1 passes/h; F = 8.93, *d.f.* = 1, P = 0.003). A significant interaction was found between year and habitat type (F = 2.81, *d.f.* = 3, P = 0.041); therefore, data were analyzed separately by year. For both years, bat activity was greatest at medium and large stream sites, intermediate at small stream sites, and least at upland sites (Table 1).

In both 1996 and 1997, mean bat activity differed among habitats, among sampling blocks nested within habitats, and among 2-week sampling periods (Table 2). In 1996, small streams and upland habitats differed from one another and from medium and large stream sites. The difference between medium and large stream sites was not significant (Table 3). In contrast to results from 1996, no difference was found between small stream and upland sites in 1997 (Table 3). Consistent with results from 1996, differences were found between upland and medium stream sites, upland and large

TABLE 2.-Results from analysis of variance of mean number of bat passes per hour by year during the first 3 h after sunset among habitats, sampling blocks nested within habitats, and 2-week sampling periods in the Pilot Creek study area, Six Rivers National Forest, California. Data were log transformed, ln(bat passes per hour + 1), for analysis.[a]

Year	Source	*d.f.*	Adjusted *SS*	Adjusted *MS*	*F*	*P*
1996	Habitat	3	71.999	23.666	27.61	<0.001
	Block (habitat)	12	38.503	3.209	3.74	<0.001
	Sampling Period	4	46.872	11.718	13.67	
	Error	96	82.285	0.857		
	Total	115				
1997	Habitat	3	81.677	27.226	33.99	<0.001
	Block (habitat)	12	48.744	4.062	5.07	<0.001
	Sampling Period	6	127.920	21.320	26.62	<0.001
	Error	119	95.319	0.801		
	Total	140				

[a] *SS*, sum of squares; *MS*, mean squares.

stream sites, small and medium stream sites, and small and large stream sites.

Bat activity varied widely among sites within each stream size class. For example, mean bat passes/h was 1.2-25.8 at upland sites, 8.2-31.8 at small stream sites, 25.2-88.4 at medium sites, and 24.7-48.0 at large stream sites. Some sites consistently had greater or lesser bat activity, whereas others varied by night. For example, 1 medium stream site had a mean of 1 bat pass/h during the first 3 hours after sunset on 21 August 1997, and 32.3 passes/h the following night.

No correlation was found between number of bat passes/h and minimum (r^2 = 0.010, *d.f.* = 1, P = 0.15) or maximum (r^2 = 0.002, *d.f.* = 1, P = 0.50) 24-h temperature. Also, no correlation was found between mean bat activity and channel width at sampling sites (r^2 = 0.007, *d.f.* = 1, P = 0.19).

Two hundred seven bats comprising 7 species were captured, including 4 species that were formerly candidates for endangered species listing and 3 current California Department of Fish and Game "Species of Special Concern" (Table 4). The 3 most commonly captured species were California myotis (*M. californicus*), long-eared myotis

TABLE 3.--Results from Tukey post-hoc multiple comparisons of mean bat activity among habitats by year in the Pilot Creek study area, Six Rivers National Forest, California. Data were log transformed, ln(bat passes per hour + 1), for analysis.

Year	Habitat	Statistic	Small stream	Medium stream	Large stream
1996	Upland	*t*	-3.44	-7.05	-7.80
		P	0.005	<0.001	<0.001
	Small stream	*t*		4.80	5.88
		P		<0.001	<0.001
	Medium stream	*t*			1.15
		P			0.659
1997	Upland	*t*	-1.84	-8.60	-7.20
		P	0.258	<0.001	<0.001
	Small stream	*t*		6.91	5.15
		P		<0.001	<0.001
	Medium stream	*t*			-2.36
		P			0.091

TABLE 4.--Numbers of bats captured by stream size in the Pilot Creek study area, Six Rivers National Forest, California, June-August, 1996 and 1997.[a]

Habitat	*M. califor-nicus*	*M. evotis*	*M. volans*	*M. thysanodes*	*L. nocti-vagans*	*C. townsendii*	*E. fuscus*
Medium streams[b]							
Total captured	32	21	6	2	0	2	0
Males	10	15	0	1		2	
Females	22	6	6	1		0	
Adults	29	21	6	2		2	
Juveniles	3	0	0	0		0	
Large streams[c]							
Total captured	73	9	12	13	30	6	2
Males	41	9	4	3	29	0	2
Females	32	0	8	10	1	6	0
Adults	49	9	10	9	28	6	2
Juveniles	22	0	2	4	2	0	0
Total number captured	104	30	18	15	30	8	2
Status[d]		ESA	ESA, CFG	ESA, CFG		ESA, CFG	

[a] *M., Myotis; L., Lasionycteris; C., Corynorhinus; E., Eptesicus.*
[b] 64 captures, 20 capture nights, 47.75 net hours, 3.2 captures/night, 1.34 captures/net hour.
[c] 142 captures, 28 capture nights, 84.83 net hours, 5.1 captures/night, 1.67 captures/net hour.
[d] ESA, former federal endangered species candidate; CFG, California Department of Fish and Game "Species of Special Concern."

(*M. evotis*), and silver-haired bat (*Lasionycteris noctivagans*). Townsend's big-eared bat (*Corynorhinus townsendii*) and big brown bat (*Eptesicus fuscus*) were rarely captured. No bats were recaptured on the same night.

More male long-eared myotis and silver-haired bats were captured than females (Table 4). No female big brown bats were captured. More females than males were captured among California myotis, long-legged myotis (*M. volans*), fringed myotis (*M. thysanodes*), and Townsend's big-eared bat. Juveniles of 4 species were captured, includeing California myotis, long-legged myotis, fringed myotis, and silver-haired bat. The total number of bats captured increased throughout the 3-month season, peaking in August during both years (1996-1997 combined: June, n = 24; July, 66; August, 117).

Numbers of bats captured between medium and large streams seemed to vary by species, although small samples of mist-netted bats did not warrant statistical tests. Among 6 species, at least twice as many bats were captured at large streams, whereas 1 species was captured more often at medium streams (Table 4). However, it is important to note that that trend was less distinct when one considers the number of captures per net hour versus captures per night.

DISCUSSION

All stream sites sampled were used by bats, some at much higher rates than upland sites. Larger-sized streams seemed to be an important resource for bats. One telemetry study also found this to be the case: female Ozark big-eared bats (*C. townsendii ingens*) foraged more frequently along edges of intermittent streams and mountain slopes than expected based on availability of habitats (Clark et al. 1993). In our study, we found that streams with discontinuous water had similar amounts of bat activity as streams with continuous standing water. This may be because bats require standing water for drinking (Cross 1986). Larger-sized streams provide standing water, whereas smaller intermittent streams are dry for most of the year. Bats also may spend more time along larger streams foraging for insects. Greater abundances of insects have been found over water compared with along paths or in the forest (Barclay 1991). Greater abundances of insects in riparian habitat compared with adjacent forests also have been reported (Thomas 1988). Larger streams tend to have wider gaps in the forest canopy, which we hypothesize may facilitate travel and foraging by bats.

Our results apply only to the first 3 h of the night because our analyses used the mean number of bat passes per hour during the first 3 h after sunset. However, ancillary information suggests this time period is representative of the entire night. We found the same pattern of bat activity among habitats using the entire nocturnal period or only the first 3 h after sunset (Seidman 1999). Therefore, although bat activity can be highly variable within a single night, it probably did not affect patterns that we observed.

We found a seasonal increase in summer bat activity but no effect of temperature. Temperature and time of year have been found to influence bat activity (Rydell 1991; Walsh and Mayle 1991). Bat activity was greater later in summer in the Oregon Coast Range (Hayes 1997). In late summer, bat activity may be greater because of higher temperatures, young-of-the-year foraging, and greater prey availability because maximum productivity of temperate-zone insects occurs in late summer (Black 1974; Williams 1961). Densities of flying insects are known to increase with temperature (Taylor 1963; Williams 1940).

We found bat activity to be highly variable among sampling nights and among sites. These results are similar to those of other studies of bat activity (Fenton 1970; Fenton et al. 1973; Hayes 1997; Krusic et al. 1996). Studies using radiotelemetry have found that many bat species, such as long-legged myotis, fringed myotis, California myotis, long-eared myotis, and big brown bats, switch roosts regularly (Brigham et al. 1997; Rabe et al. 1998). This may explain some of the variability that we encountered in bat activity among nights and locations in our study. Our results, along with those of other researchers, suggest that bat sampling over short durations may not yield accurate information regarding relative abundance or habitat use.

Bat detectors have several limitations when used to survey bat activity. Not all bat calls are sampled equally (Fenton and Bell 1981; Fenton et al. 1973). For example, bats that echolocate at lower frequencies or higher intensities are detected at greater distances than those species with higher frequencies or lower intensities (Fenton 1982; Fenton and Bell 1981; Fenton and Fullard 1981; Griffin 1971; Hickey and Neilson 1995; Limpens and Kapteyn 1991; Neuweiler 1989). Individuals of the same species may exhibit differences in call frequency, duration, and interval depending on whether they are foraging alone or with conspecifics (Obrist 1995). In some situations, bats may not use echolocation to hunt prey (Fenton 1982, 1990), thus causing activity levels to be underestimated. Species and age-groups using a given stream site also may influence perceived patterns of bat activity. Younger inexperienced bats may require more passes to obtain food and water. Larger-bodied bats require more water than their smaller-bodied counterparts, perhaps necessitating a larger-bodied bat to make more passes at a water hole than a smaller-bodied bat. Therefore, the possibility exists that sites with more juveniles or higher numbers of larger-bodied bats may exhibit more bat activity as a result of disproportionate numbers of these 2 groups. Atmospheric attenuation also is a factor affecting detection of bat echolocation calls (Griffin 1971; Lacki 1984; Lawrence and Simmons 1982; Neuweiler 1989; Thomas et al. 1987). However, differences in detectability of bat calls due to weather in our study were likely consistent across habitat types because of the use of a block design. Despite limitations described above, differences in bat detection likely were consistent across all habitats sampled.

Our study sampled bat activity below the canopy of the forest. A different pattern of bat use of intermittent streams might have been revealed if sampling had been conducted within and above the forest canopy. Some studies have found no differences in number of bat detections on the ground compared with 9 m or 30 m high in the forest canopy (Lance et al. 1995; Thomas 1988). However, another study found differences in activity levels for some forest types and species (Kalcounis et al. 1999).

All 7 species captured are thought to be associated with late-successional or old-growth forests of the Pacific Northwest (United States Department of Agriculture, Forest Service 1993). California myotis, long-legged myotis, fringed myotis, and Townsend's big-eared bat seemed to be reproducing in the Pilot Creek watershed because juveniles and lactating females were captured. Long-eared myotis was probably reproductive in the study area because lactating females were captured, even though no juveniles were observed. No evidence of reproduction was found for big brown bats because no juveniles or lactating females were captured. However, silver-haired bats had a sex ratio in our study area highly skewed toward males. Only 1 female silver-haired bat was captured throughout both field seasons (a juvenile) compared with 29 males, suggesting absence of reproduction in this species.

Our study indicated that stream sites with channel widths >1.8 m had significantly more bat activity than upland sites or stream sites with channel widths <1.2 m. Stream channels that had any water at all (even puddles) were used at much higher rates than dry channels or upland sites. However, it is important to note that bat roosts may be in upland locations, so riparian protection alone does not guarantee protection of adequate bat habitat.

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