Autumn roost-site selection by male hoary bats (*Lasiurus cinereus*) in northern California

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Effective conservation and management of a species relies upon understanding its habitat throughout its full annual cycle. For hoary bats, *Lasiurus cinereus*, their ecology is largely known from summer with the exception that they move long distances during autumn and spring and maintain some level of activity year-round. Autumn is a critically important period for hoary bats as they complete long-distance migrations between summer and winter range and they mate, both of which are energetically expensive. We studied hoary bat roost selection during autumn in a migratory stopover area in redwood habitat in northwestern California. We hypothesized that hoary bats select day roosts during autumn migration that minimize energetic expenditures and improve mating opportunities. We located 24 day roost sites of male hoary bats and evaluated site-level roost selection by comparing roosts with 120 random locations. We used multiple logistic regression to compare remotely sensed habitat features derived from LiDAR and other spatial data. The three most important variables for distinguishing roost from random locations were distance to creek, roads, and meadow. We speculate that selection of roosts in proximity to open spaces and flyways facilitated social behaviors related to mating that are commonly observed in this area.

Key words: Chiroptera, full annual cycle, LiDAR, migration, radiotelemetry, redwood, roost selection, *Sequoia sempervirens*, social behavior, stopover

La conservación y manejo de una especie se basan en el conocimiento de su hábitat a lo largo de todo su ciclo de vida anual. La ecología del murciélago cenizo, *Lasiurus cinereus*, es ampliamente conocida para la época de verano, además que se desplaza grandes distancias durante el otoño y la primavera, con algún grado de actividad durante todo el año. El otoño es una época crítica para la especie al completar su migración entre las áreas de verano e invierno, y además de aparearse, ambos eventos con un alto costo energético. Estudiamos la selección de refugios del murciélago cenizo durante el otoño en un área de parada migratoria en los bosques de secuoyas, en el noroeste de California. Nuestra hipótesis proponía que esta especie, durante su migración de otoño, elige refugios temporales que permiten minimizar su gasto energético y mejorar sus probabilidades de apareamiento. Ubicamos 24 refugios de descanso diario, y evaluamos la selección de sitios de refugio comparando con 120 localidades al azar. Utilizamos regresión logística múltiple para comparar características del hábitat detectadas a través de sensores remotos registrados mediante LiDAR, y otros datos espaciales. Las tres variables más importantes para distinguir los refugios de las localidades elegidas al azar fueron, distancia a arroyos, caminos y praderas. Deducimos que la selección de refugios en cercanía a espacios abiertos y rutas migratorias facilitan comportamientos sociales relacionados con el apareamiento, algo que es fácil de observar en el área.

Palabras clave: Chiroptera, ciclo anual completo, comportamiento social, LiDAR, migración, paradas, radiotelemetría, secuoyas, selección de refugio, *Sequoia sempervirens*

A comprehensive understanding of the ecology of a species requires determination of its habitat requirements throughout the full annual cycle (Marra et al. 2015). For bats in temperate areas, it is especially important to consider roosting habitat, as roost types and associated characteristics (e.g., thermal properties, proximity to foraging habitat) can vary throughout the

annual cycle. To date, studies of roost selection in temperate-zone bats have focused largely on the summer maternity season and winter hibernation (Weller et al. 2009), but few have considered the properties of roosting sites occupied in the autumn or spring.

Autumn is a critically important period when temperate bats transition from summer to winter habitats while concomitantly visiting rendezvous sites where they engage in mating behaviors (Racey and Entwistle 2000; Parsons et al. 2003, 2006; Cryan 2008; Cryan et al. 2012). During migration an individual makes multiple nested decisions when selecting habitat. Because temperate bats cover long distances and encounter multiple habitat types during autumn movements, it is reasonable that they would select habitat in a hierarchical manner (Johnson 1980; Manly et al. 2002; Limpert et al. 2007). Landscape-level habitat choices are followed by finer-resolution selections that may be based on land cover type, habitat elements, and microhabitat features. For example, migrating bats operating within their distributional range (first-order selection; sensu Johnson 1980) may use landmark features such as mountains, rivers, or riparian areas, to guide navigation over long distances (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009). Bats then select stopover sites after each leg of migration (second-order selection), roost trees within the stopover site (third-order), and specific locations in or on the roost tree that are chosen based on microclimate, protection from predation etc. (fourth-order selection).

Thermoregulation is considered a primary driver of roost-site selection in temperate bats (Boyles 2007; Otto et al. 2016). For example, reproductive females select roosts during summer that offer warm temperatures and protection from the elements to facilitate gestation and postnatal growth of young (Willis and Brigham 2005; Klug et al. 2012). Bats of both sexes select winter roosts that maximize the benefits of torpor (Boyles et al. 2007). During autumn, when temperate-zone bats migrate and use stopover sites (McGuire et al. 2012), roost-site selection may be more important than prey availability at stopover sites as bats make frequent use of torpor to limit energy expenditures (Cryan and Wolf 2003; Dunbar 2007). Torpor confers savings of energy and water loss (Szewczak and Jackson 1992), but arousal from torpor has significant metabolic costs (Thomas et al. 1990). To mitigate this cost, tree-roosting bats select roosts where they can exploit solar-assisted rewarming through direct sunlight exposure (McGuire et al. 2014).

Reproductive considerations may also drive habitat selection by bats during autumn. The solitary tree-roosting hoary bat (*Lasiurus cinereus*) segregates sexually during summer and is thought to mate at rendezvous sites along autumnal migratory routes (Cryan et al. 2012). Male hoary bats captured during the autumn exhibit physical indications of mating readiness, including sperm in the caudae epididymides and enlargement of accessory sexual glands (Cryan et al. 2012). Specific locations where mating occurs have not been determined although seasonal range maps indicate that they may occur in California (Cryan 2003). It is likely that mating occurs in dispersed locations, consistent with their noncommunal roosting habit. Cryan and Brown (2007) proposed that habitat selection along the migratory route may guide male and female bats to rendezvous locations, perhaps via conspicuous landmark features such as emergent trees. Once at these sites, hoary bats may select roosts in proximity to emergent trees, flyways, or other areas that improve mating opportunities.

We conducted a study of male hoary bat day roost selection at a site where they are present in high densities during autumn. In the hierarchical scheme of habitat selection that transitions from landscape (first-order) to microhabitat features (fourth-order) we considered this third-order selection (Johnson 1980). We expected that hoary bat roost selection during autumn would need to balance the competing objectives of reducing energetic costs of migration while increasing mating opportunities. We thus predicted that hoary bats would select roosts that facilitated use of diurnal torpor. In particular, a roost that remained cool during the first part of the day and then allowed passive rewarming in the afternoon would maximize torpor benefits (McGuire et al. 2014). Hence, we considered habitat variables such as elevation, slope aspect, solar radiation, and emergence of the roost tree from the canopy that might influence the roost microclimate. In addition, we considered variables that may allow male hoary bats to increase mating opportunities, including trees that extended above the canopy where bats may aggregate and distance to open areas such as meadows and stream corridors where hoary bats had been observed engaged in social interactions (Corcoran and Weller 2018).

Materials and Methods

Study area.— We conducted our study within the Bull Creek watershed of Humboldt Redwoods State Park (HRSP), Humboldt County, California (40°20′60″N, 124°0′36″W). We selected this study site because we expected to reliably capture male hoary bats during autumn (Weller et al. 2016). HRSP contains some of the largest remaining stands of old-growth coastal redwood (*Sequoia sempervirens*). Dominant tree species in post-logging areas of the park include second-growth coastal redwood, Douglas fir (*Pseudotsuga menziesii*), tanoak (*Notholithocarpus densiflorus*), red and white alder (*Alnus* sp.), and Pacific madrone (*Arbutus menziesii*). Much of the watershed is bisected by a road that parallels the creek. Several unpaved roads in the watershed begin from this road providing access to higher elevations used for recreation and fire suppression.

Bat capture.— We captured bats using standard 2.6-m nylon mist-nets in a triple-high configuration at multiple locations along an approximately 5-km section of Bull Creek. During autumn the creek bed becomes nearly dry and bats were captured over the channel. Mist-netting began at sunset and continued for 3.5 h or until enough bats had been captured to meet the quota of tags designated for use on a given night. We recorded species, age, sex, reproductive status, body measurements, and mass of all captured bats prior to release. We held hoary bats a minimum of 1 h after the time of capture to collect guano that would record foraging prior to capture (Roswag et al. 2012).

Device type and tag attachment.— We used a variety of devices to determine roost locations and attached them according to mass of device and their expected battery life. During 2017 and 2018 we used standard VHF transmitters of two different sizes (Blackburn Transmitters, Nagodoches, Texas; mass: 0.3 and 0.6 g) and attached them by trimming the hair between the bats' scapulae and affixing the transmitter with a small amount of surgical adhesive to the individuals' dorsum (Amelon et al. 2009). Standard VHF tags averaged 1.2 and 2.6% of each individuals body mass, respectively. During 2017 we used long-term VHF transmitters (model Ag392, Lotek Wireless, Newmarket, Ontario, Canada; mass = 1.3 g) that had battery durations of up to 8 months and averaged 5.7% of individual mass of bats. We attached long-term transmitters using dissolvable sutures, a safe and effective method of long-term transmitter attachment on bats (Castle et al. 2015). During 2018 we obtained additional roost locations by tracking bats that had VHF transmitters (Holohil LB-2X, Carp, Ontario, Canada) attached to a tag that recorded bat vocalizations (Corcoran et al. 2021). These combination audio and VHF tags had a mass of 2.9 g representing, on average, 11.9% of bat mass. These tags were attached to the fur on the lower dorsum of bats using small amounts of surgical glue such that tags would detach after several days. We also included day roost locations of male hoary bats from GPS locations obtained at noon during 2014–2016 (Weller et al. 2016). Animal handling and transmitter attachment protocol was approved by the Institutional Animal Care and Use Committee of the USDA Forest Service (IACUC no. 2017-014).

Locating roosts.— We used detections of VHF transmitters from a stationary data-logging receiver, scans of active frequencies using a vehicle-mounted omnidirectional antenna, and triangulation of signals using a handheld 3-element Yagi antenna from designated scanning locations to inform searches for hoary bat roosts. We installed an autonomous data-logging VHF receiver (model SRX-800; Lotek Wireless Inc., Newmarket, Ontario, Canada; air-to-ground detection range: approximately 5 km) at a location chosen to optimize detection of transmitters in the Bull Creek watershed. The data-logging receiver operated 24 h per day and without failure from 23 September 2017 through 10 May 2018. The stationary receiver consisted of a three 5-element Yagi antenna (Lotek Wireless Inc., Newmarket, Ontario, Canada) elevated on a 5-m pole, solar panel, 12-volt battery with a charge controller, and a weatherproof enclosure housing the receiver. The three antennae were oriented 120° relative to one another to determine the azimuth of detections. The receiver was programmed to scan each active frequency on each antenna for 15 s before switching to the next active frequency. We drove roads daily and scanned transmitter frequencies from preestablished lookouts that provided good telemetry vantage points to determine presence of tagged individuals in the study area. We located roosts by tracking signals on foot with handheld radiotelemetry receivers (model SRX-D800, Lotek Wireless Inc., Newmarket, Ontario, Canada; model R-1000, Communications Specialists, Orange, California) using a homing technique (Amelon et al. 2009). Once the vicinity of the signal was determined, the roost

site was identified by incrementally decreasing search area and walking 360° around the source of the signal. Due to canopy height and structural complexity of the forest in HRSP, it was often difficult to unequivocally determine the exact tree in which the bat was roosting. As a result, we identified roost sites as the 0.1-ha circular plot centered on the most likely roost tree. For roost sites determined via GPS, we used coordinates of the fix location as plot center.

Generating random locations.— Random locations were generated within a subsection of HRSP where 1-m remotely sensed light detection and range (LiDAR) data were available and in which all bat roosts had been located. We further restricted random locations such that they did not occur in terrain where we were unlikely to detect signals from transmitters due to distance from monitoring points and steep topography. We used ArcGIS (ESRI 2019) to create a VHF coverage map that reflected our ability to receive signals from transmitters from our scanning locations along roads and prominent overlooks. We generated a VHF coverage map by including: (i) 1-km buffers around roads; (ii) 1-km buffers around high-elevation lookouts where telemetry scans were conducted regularly; and (iii) 5-km viewshed analysis from high-elevation lookouts. We calculated viewsheds using the Spatial Analyst tools in ArcGIS using an offset height of 2 m above the ground from lookout location and 5 m above the ground for the stationary telemetry tower. To create a representative sample of random locations across the study area, we generated five random locations per roost (Northrup et al. 2013; Neubaum 2018).

Habitat variables.— We considered the following variables to distinguish hoary bat day roosts from random locations: forest stand type, elevation, slope aspect, maximum canopy height, canopy emergence, distance to road, distance to meadow, distance to Bull Creek, daily solar radiation, AM solar radiation, and PM solar radiation.

Canopy height, canopy emergence, elevation, and aspect data were extracted from 1-m LiDAR data collected in 2007 by California State Parks. Solar radiation was calculated in ArcMap with the Area Solar Radiation tool in the Spatial Analyst Toolbox. Solar radiation is widely used as a surrogate index for roost warmth in studies of bat roost selection (Menzies et al. 2016) and roost warmth is frequently used to explain the energetics of roost selection. We used the Euclidian distance tool in the Spatial Analyst Toolbox to determine distance to nearest meadow, creek, and road. We quantified canopy emergence by subtracting mean canopy height from a 10-ha plot from the maximum canopy height of a nested 0.1-ha plot. For these calculations we limited canopy height to values above 10 m to prevent shrubs and ground values from factoring into mean canopy height. We classified whether each 0.1-ha plot was redwood-dominant forest using a 2010 California State Parks vegetation map.

Statistical analysis.— We included every roost site that we found in our analyses. Although inclusion of >1 roost per individual may not necessarily represent independent selection, inclusion of multiple roosts from some individuals is commonly done to increase sample sizes and thus statistical

power in studies of bats (Amelon et al. 2009). Each roost was used once in analyses regardless of how many days that roost remained occupied.

To avoid problems with multicollinearity, we removed variables that had a correlation coefficient > 0.7, retaining the variable that we considered more likely to be ecologically significant. Elevation and distance to creek were highly related ($r = 0.78$), as were canopy emergence and canopy height ($r = 0.85$). We removed elevation and canopy height from consideration in our model. We used univariate logistic regression to compare hoary bat roost locations with random locations. If a univariate model had an Akaike Information Criterion (AIC; Burnham and Anderson 2002) value greater than the null model, we did not consider that variable in multiple regression models (Carter and Feldhamer 2005; Slinker and Glantz 2008). For example, we used univariate models to determine which of three measures of solar radiation to include in multiple regression models.

We used multiple logistic regression to find the combination of variables that best distinguished roosts from random locations. We included all possible subsets of remaining variables in the set of models we considered. A balanced model set is necessary to determine relative importance values among variables under consideration (Burnham and Anderson 2002). We averaged models that comprised 95% of model weights to determine parameter estimates and relative importance of each variable using the R package MuMIN (Burnham and Anderson 2002; Symonds and Moussalli 2011; R Core Team 2019).

We tested whether roosts found using VHF telemetry were biased toward more easily accessible areas compared to those determined via GPS where access issues were not a factor. We used Tukey's Honest Significant Difference test to compute a multiple comparison between VHF- and GPS-determined roosts for elevation, distance to roads, and distance to meadows.

RESULTS

We located 24 roosts for 16 different male hoary bats. We found 18 roosts from 13 bats using ground-based VHF telemetry: five using standard VHF tags, eight from long-term tags, and five from those attached to acoustic tags. The remaining six roosts from three bats were determined from GPS tags (Table 1). Multiple roosts from the same individual were 70–3,025 m apart.

Univariate analyses comparing hoary bat roost plots ($n = 24$) and random locations ($n = 120$) eliminated AM solar radiation, PM solar radiation, slope, and slope aspect from consideration in multiple logistic regression models (Table 2). Distance to creek, distance to meadow, distance to road, solar radiation, canopy emergence (Fig. 1), and the indicator variable for redwood forest were retained for multiple regression models.

The highest-ranking model for hoary bat roost selection among the 64 we evaluated included distance to creek, meadow, road, and canopy emergence (Table 3). However, there was high model uncertainty with 13 models within three AIC points of the top model and comprising 95% of the total Akaike weights of all models. Nevertheless, three variables stood out as important for distinguishing roost from random sites. Distance to Bull Creek and distance to road both had parameter estimates with confidence intervals that did not overlap zero and each contributed to all 13 of the models in the top model subset (Table 4). Distance to meadow had a relative importance of 0.72 and contributed to 8 of 13 highly ranked models.

Using model-averaged parameter estimates, we calculated that, adjusted for the effects of other covariates, an increase of 500 m from Bull Creek reduced the probability of a roost occurring by 14.5% (Fig. 2). Similarly, adjusting for other variables included in the averaged model, an increase of 500 m from meadows decreased probability of a roost occurring by 12.7% and roost probability decreased 37.8% 500 m from roads. An increase of 10 m of canopy emergence increased the probability of a roost occurring by 11.7%.

Most of the roost sites, regardless of the method we used to locate them, were close to the main paved road that paralleled Bull Creek and bisected our study area. However, we determined that roosts found using ground-level VHF telemetry were not significantly closer to roads than those determined

Table 1.—Twenty-four roosts were located for 16 hoary bats (*Lasiurus cinereus*) in Humboldt Redwoods State Park, Humboldt County, California. We used four different tag types including GPS and three different types of VHF transmitters.

Bat ID/freq.	Year	No. of roosts	Minimum distance between roosts (m)	Tag type
479	2014	1	—	GPS
40576A	2015	4	296	GPS
41276	2016	1	—	GPS
164.075	2017	1	—	Long-term VHF
164.615	2017	2	70	Long-term VHF
165.106	2017	1	—	Long-term VHF
165.305	2017	2	1,513	VHF
165.455	2017	2	2,941	VHF
165.615	2017	1	—	Long-term VHF
165.756	2017	1	—	VHF
163.991	2018	1	—	Acoustic + VHF
164.361	2018	1	—	Acoustic + VHF
164.867	2018	1	—	Acoustic + VHF
165.462	2018	1	—	Acoustic + VHF
164.798A	2018	2	1,726	Acoustic + VHF
164.798B	2018	2	3,025	Acoustic + VHF

Table 2.—Mean values, standard error (*SE*), and range of male hoary bat roosts (*n* = 24) and random locations (*n* = 120) in Humboldt Redwoods State Park, Humboldt County, California. Akaike Information Criterion (AIC) values are from univariate logistic regression models of habitat variables. Models with asterisk (*) improved fit compared to the null model (AIC$_{(null)}$ = 131.8) and were retained for multivariate models.

| Variable	Roost site			Random site			AIC
	Mean	*SE*	Range	Mean	*SE*	Range	
Distance to Bull Creek (m)	615.9	162.5	33.9 to 2,692.3	1,727.3	98.7	42.6 to 4,398.6	109.05*
Distance to road (m)	161.3	27.1	0.0 to 454.0	373.8	31.3	0.1 to 1,464.5	121.10*
Distance to meadow (m)	345.9	63.0	14.8 to 1,182.6	791.2	71.5	11.7 to 3,455.3	122.78*
Daily solar radiation (h/day)	9.3	0.1	7.5 to 9.9	8.7	0.1	3.1 to 9.9	127.54*
Canopy emergence (m)	27.1	2.2	11.8 to 51.3	21.6	0.9	−6.6 to 48.3	129.05*
Redwood habitat (prop of 0.1-ha plots)	0.4	—	0.0 to 1.0	0.3	—	0.0 to 1.0	131.44*
PM solar radiation (h/day)	5.4	0.1	3.6 to 5.9	5.2	0.1	1.0 to 5.9	131.91
AM solar radiation (h/day)	5.3	0.1	4.0 to 5.9	5.1	0.1	0.0 to 5.9	132.87
Slope	22.4	2.6	1.7 to 42.0	22.8	1.0	1.5 – 67.0	133.73
Slope aspect (dev. from 225, degrees)	48.6	18.2	−100.7 to 210.1	49.6	9.1	−127.6 to 223.7	133.76
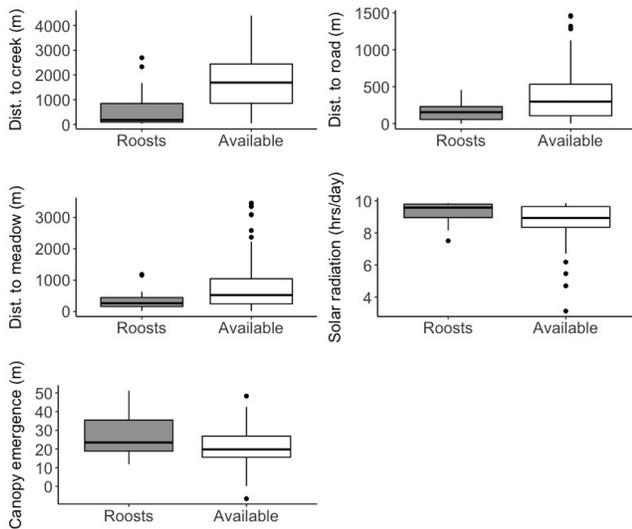
Fig. 1.—Boxplots showing quartile values of habitat variables that improved the null model in univariate regressions between hoary bat (*Lasiurus cinereus*) roost sites (*n* = 24) and random locations (*n* = 120) in Humboldt Redwoods State Park, Humboldt County, California. The upper and lower and upper box boundaries the 25th and 75th percentiles, respectively, and the centroid line inside box represents the median.

using GPS (*P* = 0.503; Fig. 3). We also found no difference in distance to Bull Creek (*P* = 0.174) or distance to meadow (*P* = 0.518) between roost sites found using VHF versus those found with GPS.

DISCUSSION

We determined that, during autumn, male hoary bats selected roosts in closer proximity to Bull Creek, roads, and meadows than random locations. Each of these variables represents relatively open spaces that hoary bats are likely to utilize as flyways (Loeb and O'Keefe 2011). In particular, we found proximity to the creek and roads were the most important variables for discriminating hoary bat roosts from random locations in our study area. However, these variables are somewhat conflated as the primary road through our study site parallels Bull Creek for long stretches, in most cases <100 m away from the channel. Considered cumulatively the road–creek corridor creates a wide, somewhat linear, open space through the forest.

Our results corroborate previous studies that hoary bats select roosts in proximity to open spaces, albeit the other studies focused on lactating female roost selection during

Table 3.—Subset of 13 models comprising 95% of models weight from a candidate model set of 64 models for hoary bat roost-site selection in Humboldt Redwoods State Park, Humboldt County, California. Degrees of freedom, log likelihood, Akaike Information Criterion (AIC), difference in AIC from top model, model weight (*w$_i$*), and cumulative model weight (cum. *w$_i$*) are presented.

Model	df	LogLik	AIC	ΔAIC	*wi*	cum. *wi*
creek + road + meadow + emergence	5	−42.30	95.03	0.00	0.132	0.132
creek + road + meadow + solar	5	−41.40	95.23	0.21	0.119	0.251
creek + road + meadow	4	−43.55	95.39	0.37	0.110	0.361
creek + road + solar	4	−43.56	95.41	0.38	0.109	0.470
creek + road + meadow + solar + emergence	6	−41.58	95.78	0.76	0.090	0.560
creek +road + meadow + Redwood	5	−42.78	95.98	0.96	0.082	0.642
creek +road + meadow + solar + Redwood	6	−41.91	96.43	1.40	0.065	0.707
creek + road + solar + emergence	5	−43.33	97.10	2.08	0.047	0.754
creek + road + meadow + emergence + Redwood	6	−42.27	97.14	2.12	0.046	0.800
creek + road	3	−45.62	97.41	2.38	0.040	0.840
creek + road + solar + Redwood	5	−43.52	97.48	2.45	0.039	0.879
creek + road + emergence	4	−44.79	97.88	2.85	0.032	0.911
creek + road + meadow + solar + emergence + Redwood	7	−41.56	97.95	2.92	0.031	0.942

Table 4.—Parameter estimates, adjusted standard error (*SE*), 95% confidence intervals (CIs), and relative variable importance of variables in predicting autumn roost site use by male hoary bats in Humboldt Redwoods State Park, Humboldt County, California.

	Parameter estimate	Adjusted *SE*	95% CI	Relative importance
(Intercept)	−2.1355	3.9461	−9.8697 to 5.5987	—
Distance to Bull Creek	−0.0012	0.0003	−0.0019 to −0.0005	1.00
Distance to road	−0.0040	0.0016	−0.0070 to −0.0009	1.00
Distance to meadow	−0.0007	0.0006	−0.0021 to 0.0002	0.72
Solar	0.3136	0.4316	−0.2576 to 1.4385	0.53
Emergence	0.0161	0.0297	−0.0284 to 0.1090	0.40
Redwood indicator	0.1379	0.4618	−1.0091 to 1.9986	0.28
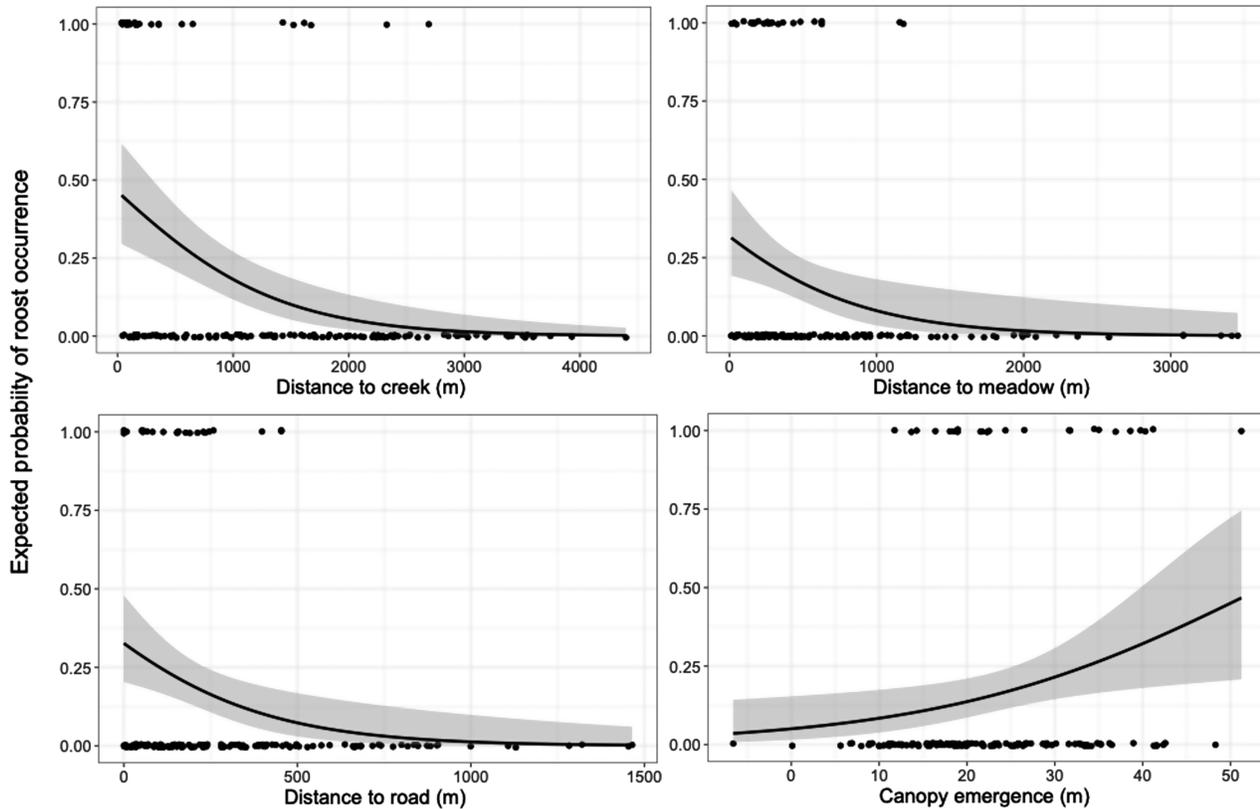
Fig. 2.—Continuous variables from the most highly ranked model fit with a logistic regression curve to show probability of roost occurrence with respect to the range of the continuous variable. Data points at 1 represent hoary bat (*Lasiurus cinereus*) roosts and those at 0 represent random sites in the study area, generated for comparison.

summer (Constantine 1966; Willis and Brigham 2005; Klug et al. 2012). A study of *L. cinereus* and *L. borealis* in Iowa found that, almost invariably, both species selected roosts along forest edge whether that edge was a meadow or an agricultural field (Constantine 1966). Landscape-scale summer roost selection studies of *Lasiurus* in Arkansas found that both males and females tend to roost in thinned forests with less dense vegetation (Perry and Thill 2007; Perry et al. 2007). Potential reasons that bats select more open forests include ease of maneuverability and roost relocation. The large size and high wing loading of hoary bats render them less maneuverable than many smaller species and they therefore require larger open spaces for foraging and movement (Shump and Shump 1982). Although the roosts we located were proximate to open spaces, they were not necessarily adjacent. Roosts

were often located in areas with cluttered canopy and understory vegetation.
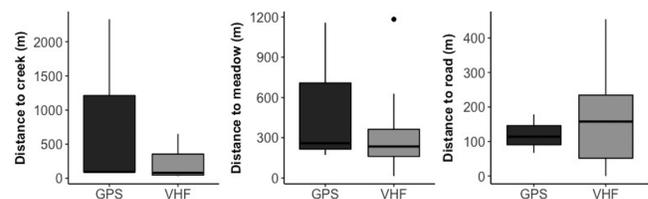
Fig. 3—Boxplots showing quartile values of hoary bat (*Lasiurus cinereus*) roosts found by GPS location (*n* = 6) and by VHF ground-based telemetry (*n* = 18) for the variables of greatest importance across averaged models, distance to Bull Creek, meadows, and roads. Humboldt Redwoods State Park, Humboldt County, California.

Klug et al. (2012) suggested that female hoary bats select roosts near open areas as it provides easier access to the open spaces they use to forage. This explanation may be less relevant in our study because hoary bats do not appear to be regularly foraging in our study area. During September and October of 2017 and 2018 only 62 of 352 (17.6%) of hoary bats captured produced guano when held for at least an hour after capture. Although digestive retention time during autumn has not been documented in hoary bats, it is generally considered to be less than 1 h in insectivorous bats (Roswag et al. 2012) and guano samples were obtained from male and female hoary bats during spring migration when they were held for only 15 min (Valdez and Cryan 2009). The hours immediately following sunset are generally considered a productive foraging time for most species of bats (Rydell et al. 2006). Hence, we would expect the hoary bats captured in our study to have produced guano if they had actively foraged prior to capture. Lack of evidence of foraging suggests that other behavioral motives, presumably mating competition, may explain the notable amount of hoary bat activity in Bull Creek during the autumn and may influence roost selection.

Ninety-five percent of hoary bats captured from 2010 to 2018 (*n* = 1,309) in the Bull Creek watershed were male (T. Weller, USDA Forest Service, Pacific Southwest Research Station, Arcata, California, personal communication, September, 2018). However, it is unclear whether this reflects the true sex ratio at our study site during autumn. Male hoary bats engage in chasing behaviors in the flyway above Bull Creek during autumn and frequently reduce their use of echolocation (Corcoran and Weller 2018; Corcoran et al. 2021). This may result in a capture bias toward males as their competitive behavior may render them more susceptible to capture. More relevant to results presented here, such behaviors are likely more successful in open habitats, such as above meadows, in stream corridors, and along roads, where bats would have reduced risk of collision with clutter objects. Roost selection in proximity to open flyways would facilitate these behaviors.

Bias in our ability to detect transmitters offers another possible explanation for our finding of bats roosting near open areas. Proximity to roads certainly facilitates access by researchers and improves probabilities of locating roosts. Nevertheless, we determined that roosts located using handheld VHF telemetry were not closer to roads than those located via GPS indicating that, rather than a methodological issue, hoary bats selected roosts for their proximity to roads. Such methodological biases are likely inherent to most studies that use ground-to-ground VHF searches in densely forested areas and steep terrain, but few studies have attempted to quantify these biases. Further, we limited our designation of available sites within the watershed to where our reception model predicted we would be likely to detect VHF signals from transmitters; that is, we excluded available sites far from roads, yet still found differences between bat roosts and random locations. Limiting available habitat to only those areas where animals are observable with available techniques has recently been used to avoid some biases that previously have gone uncorrected in wildlife habitat selection studies (Holloran et al. 2015; Metz et al. 2020).

Species like hoary bats that are adapted to flight in open spaces regularly roost near roads and edges (Loeb and O'Keefe 2011). Presumably hoary bats in our study use roads and meadows as commuting or activity areas, though we did not survey bat activity in these areas. Roost sites should also have been easier to locate using ground-based telemetry near Bull Creek which runs parallel to the primary road through the park and near meadows where signal obstructions from dense forests were minimized, but we did not find a significant difference between roost location methods for these variables. Because we tagged bats that we captured along Bull Creek, it may seem unsurprising that we located roosts nearby. However, a roost anywhere in our study area should have allowed hoary bats access to the creek and other open flyways with minimal energy expenditure. Indeed, one of the bats used in this study sometimes made single-night 70-km journeys to an alternate roost area (Weller et al. 2016).

It has been proposed that hoary bats may be attracted to the tallest trees in a landscape as potential mating or lekking sites (Cryan and Brown 2007; Cryan 2008; Cryan and Barclay 2009). Thus, during migration, bats may investigate areas with tall trees or emergent canopy and may select such areas as stopover sites (second-order selection) that may facilitate mating opportunities. As the only major aggregation site of hoary bats during autumn yet to be documented, HRSP is likely to be a site significant to mating. However, at the third-order scale of habitat selection, we found limited evidence that tall trees were an important criterion for day roost selection within the stopover site. Day roost sites were an average of 6 m taller than the surrounding canopy compared to random sites, but canopy emergence was only the fifth most important variable for distinguishing roosts from random sites in our multivariate model. Thus, we did not find strong evidence to support the tallest tree hypothesis for day roost selection by male hoary bats at our study site.

We also did not find strong evidence that hoary bats selected roost sites based on thermal characteristics that would minimize energy expenditure while day roosting. We postulated that bats could minimize energy expenditure by selecting roosts that remained cool in the morning and facilitated passive rewarming in the afternoon to maximize benefits of torpor (McGuire et al. 2014; Neubaum 2018). In our study area, this would manifest itself as roosts at low elevations on south-facing slopes or in tall trees at low to mid-elevations. Roost sites were lower in elevation than random sites, but we did not include it in models because it was highly correlated with distance to Bull Creek (*r* = 0.78). Slope aspect was not an important criterion for distinguishing roost from random sites; bats did not select sites on southern aspects that would facilitate passive rewarming nor on northerly aspects that may allow them to use deeper torpor during the day. Our models suggested that total daily solar radiation was a more important variable than afternoon solar radiation for explaining hoary bat roost selection. And, although daily solar radiation contributed to many highly ranked models, the confidence interval of its parameter estimate overlapped zero and its relative importance was low relative to other variables we considered. Similarly, solar radiation was

not an important landscape-level variable explaining autumn roost selection by little brown bats in Colorado (Neubaum 2018). Past studies of forest-dwelling bats that explained roost selection on the basis of thermal or energetic requirements have used tree height, roost aspect, and surrounding canopy cover as proxies for the amount of solar radiation at the roost (Willis and Brigham 2005; Klug et al. 2012). Solar radiation is increasingly estimated directly rather than via proxy variables that may be correlated with solar exposure (Neubaum 2018) and we employed that technique in our study. As availability of LiDAR data expands in coming years, this method will likely become more common for quantification of solar exposure on roosts or dens of mammals. However, it should be noted that solar radiation too is only an index of the thermal characteristics of roosts that would be better measured directly via temperature-sensitive data loggers (Boyles 2007). Owing to the challenge of placing temperature sensors in roosts and random trees and, in our study, even determining the specific location of a bat on the tree, it is likely that indices of thermal characteristics will continue to be used in many situations.

Male hoary bats in our study exhibited a weak preference for sites dominated by redwood trees. Based on previous studies of roost selection by species of *Lasiurus* and hypotheses that hoary bats may use tall trees as landmarks for migration and mating, we expected most roost sites to occur in old redwoods because of their height. Hoary bats have been observed roosting in wide variety of tree species including short-statured species such as white spruce (*Picea glauca*), oaks (*Quercus* spp.), short-leaf pine (*Pinus* spp.), cherry (*Prunus* spp.), cypress (*Cupressus* spp.), shrubs, fruit trees, and in mixed-species deciduous forests (Dalquest 1943; Constantine 1959; Willis and Brigham 2005; Perry and Thill 2007; Klug et al. 2012; Marin et al. 2020). However, in most cases these bats were located via visual observation rather than radiotelemetry which may introduce bias as to roost heights and the types and species of trees they use.

We successfully located roosts of male hoary bats during autumn and determined characteristics that distinguished roost from random sites. Determination of roost-site selection during migration is challenging for any bat species because they tend to not spend much time in a given area (McGuire et al. 2012; Roby et al. 2019). This issue is exaggerated in migratory tree bats that may cover hundreds of km during autumn migration (Weller et al. 2016). We took advantage of a known aggregation area to gain insights into third-order roost selection by male hoary bats that was effective because we were able to tag many bats over several years. Although we were not able to assess characteristics of roost trees themselves, we determined that male hoary bats selected roosts in proximity to open flight areas that would facilitate social behaviors among individuals. Whereas previous studies of roost selection in bats have focused on the energetic consequences of roost-site selection, our results suggest that, during autumn, social and reproductive considerations may also be important determinants of habitat selection. Understanding seasonal habitat selection, and the factors that motivate it, is critical to improving appreciation of the full annual cycle of bats that is necessary to conserve these species.

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