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Abstract

The ringtail (*Bassariscus astutus*) is a species of conservation concern. Yet, little is known about basic ringtail ecology at the northwestern edge of its range, where the habitat differs considerably from its primary range in the southwestern United States. Diurnal rest sites, such as cavities in live and standing-dead trees, are an essential habitat element for ringtails and co-occurring mesocarnivores. Ringtails use diurnal rest sites as shelter during adverse weather conditions, refugia from predators such as the co-occurring fisher (*Pekania pennanti*), and dens to raise young. Understanding the forest conditions associated with rest sites selected by ringtails can inform forest management practices. We fixed very-high-frequency radio collars to 16 ringtails on the Hoopa Valley Indian Reservation in northern California to better understand the relationships between forest characteristics and fisher presence on ringtail rest-site use. We found that ringtails were more likely to select rest sites in mature older forests compared to oak woodland and open areas, and were less likely to select rest sites closer to perennial water sources. We did not detect an effect of fishers on the selection of rest sites. These results indicate that both late-seral and some early-seral forest conditions provide suitable habitat for ringtail rest sites and ultimately demonstrate that ringtails use a mosaic of seral stages in the forests of the Pacific Northwest.

Keywords: *Bassariscus astutus*, diurnal rest site, fisher, *Pekania pennanti*, ringtail

Introduction

The conservation of secretive and rare species is often hindered by a lack of basic ecological knowledge (Schemske et al. 1994, Young et al. 2016). Gaps in our understanding of life-history traits, habitat preferences, species interactions, and population-level threats often limit effective population monitoring, habitat management, and conservation planning (Hernández et al. 2006, Young et al. 2016). Medium-sized carnivorans (i.e., members of the order Carnivora ≤ 15 kg; Roemer et al. 2009) are of particular concern because these species often occur at low or unknown densities (Thornton and Pekins 2015), they have experienced geographic range contractions and population declines globally (Belant et al. 2009, Marneweck et al. 2021), and there are uncertainties about fundamental aspects of their ecology (Roemer et al. 2009, Proulx 2020, Marneweck et al. 2021). The development and success of conservation strategies for these species require a detailed understanding of their taxonomy, ecology, and threats to their persistence (Ceballos and Ehrlich 2002, Ripple et al. 2014, Marneweck et al. 2021).

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There are large disparities in our knowledge of the ecology of medium-sized carnivorans that occupy coniferous forests in western North America (Buskirk and Zielinski 2003). There has been a significant amount of research conducted on American marten (*Martes americana*), Pacific marten (*Martes caurina*), and fisher (*Pekania pennanti*) in the coniferous forests in western North America (e.g., Green et al. 2018, Matthews et al. 2019, Martin et al. 2020). However, there have been limited studies on other co-occurring medium-sized carnivorans, such as gray fox (*Urocyon cinereoargenteus*), western spotted skunk (*Spilogale gracilis*), and ringtail (*Bassariscus astutus*). For ringtails, the smallest member of the north-temperate Procyonids (Buskirk and Zielinski 2003), the coniferous forests of the Pacific Northwest represent the northernmost extent of their distribution, and the habitat greatly differs from the southern portion of their range (National Wildlife Federation 2022). In the southwestern United States and northwestern Mexico, ringtails occupy a wide variety of habitat types, such as grasslands, scrub, and shrub (Trapp 1978, Kaufmann 1982, Belluomini 1983, Ackerson and Harveson 2006, Harrison 2012). In general, few studies have been conducted on the ecology of ringtails in areas where they are common (Ackerson and Harveson 2006, Harrison 2012), resulting in limited information about their ecology, with even less known about their ecology at the periphery of their range. Although ringtails have been reported to occupy low-elevation, hardwood, and conifer-hardwood forests in northern California and southern Oregon (Callas 1987, Alexander et al. 1994), there is little information about fine-scale stand-level habitat use at the northernmost extent of their range.

Ringtails are nocturnal and use a variety of structures for diurnal resting bouts, which provide shelter during adverse weather conditions, protection from predators, and denning areas to raise young (Dalke 1948, Callas 1987, Lariviere 2004, Hwang et al. 2007). In forested environments, ringtails frequently use tree cavities for these diurnal resting bouts (Callas 1987, Alexander et al. 1994, Campbell 2004). For example, Callas (1987) found that diurnal rest sites (hereafter rest sites) in the Klamath National Forest located in northern California occurred primarily in trees, followed by rock outcroppings, with a small number found in logs. The development of tree cavities suitable for rest sites often takes decades and multiple ecological processes to develop (e.g., Michel and Winter 2009). Thus, tree cavities are often less abundant in forests managed for timber production compared to unmanaged forests (e.g., Cockle et al. 2010, Remm and Lõhmus 2011, Andersson et al. 2018) due to limitations in the ecological structures (e.g., large trees) and processes (e.g., fungal decay, insects) necessary for cavity development (Gibbons and Lindenmayer 2002). Ringtails are members of a diverse guild of medium-sized carnivorans, including fishers, that rely on, and potentially compete for, rest sites (Gabriel et al. 2015, Sweitzer and Furnas 2016, Matthews et al. 2019). It is unknown whether larger, male fishers exhibit predation pressure on ringtails. There is little information about interactions between ringtails and other medium-sized carnivorans, although Green et al. (2018) found evidence for cascading relationships between fishers, ringtails, and gray foxes, with fishers indirectly negatively affecting ringtails.

The ringtail is listed as a species of greatest conservation need in the California State Wildlife Action Plan (California Department of Fish and Wildlife 2015) and the Oregon Conservation Strategy (Oregon Department of Fish and Wildlife [ODFW] 2016). This is due to the uncertain ecological needs and conservation requirements at the periphery of its range and its cultural importance to many Indigenous communities in the western United States (Goddard 1903, Goldschmidt and Driver 1940). However, we have little information about ringtail habitat requirements and interspecies interactions at the far northern edge of its range. Previous research demonstrates diverse and sometimes conflicting habitat requirements by ringtails across their distribution, from arid portions of the primary range in the desert Southwest (Trapp 1978, Kaufmann 1982, Ackerson and Harveson 2006) to temperate forests along the Pacific coast (Callas 1987). Extrapolating observed associations from the rest of their range to the unique habitat conditions of the inland Pacific Northwest may lead to non-optimal management recommendations (Davies et al. 2013, Holbrook et al. 2017). For example, a noticeable difference between the arid Southwest and the Pacific Northwest is the availability of perennial water sources, which have been described as important drivers of ringtail habitat selection (Trapp 1978, Lacy 1983, Chevalier 1989). Land managers and biologists require information on ringtail habitat selection to implement and monitor conservation actions for ringtails, particularly in forests experiencing changes in wildfire frequency and intensity, undergoing active fuels management, and managed for timber production (ODFW 2016). Understanding the forest conditions that support rest sites selected by ringtails would contribute to their conservation in managed forests.

We investigated rest-site selection of ringtails as a function of forest stand composition and characteristics, water availability, and interspecific interactions with fishers in a forest managed for timber production and ecological and cultural resources in northwestern California. Since 1994, the Hoopa Tribe has managed timber resources on the Hoopa Valley Indian Reservation using an uneven-aged management system and regeneration methods, limiting managed stands to < 10 ha, and retaining 12 green trees > 50 cm diameter at breast height (DBH) per hectare, and all snags that do not pose a safety hazard. Understanding ringtail space use and the desirable traits of areas selected for daily activities, such as rest sites, are essential steps in designing effective conservation and management plans. This study is the first to describe diurnal rest-site selection of ringtails in the northwest periphery of their range as a function of forest species composition, forest age, availability of water, interference competition with fishers for cavity rest sites, and predation pressure exerted on them by fishers.

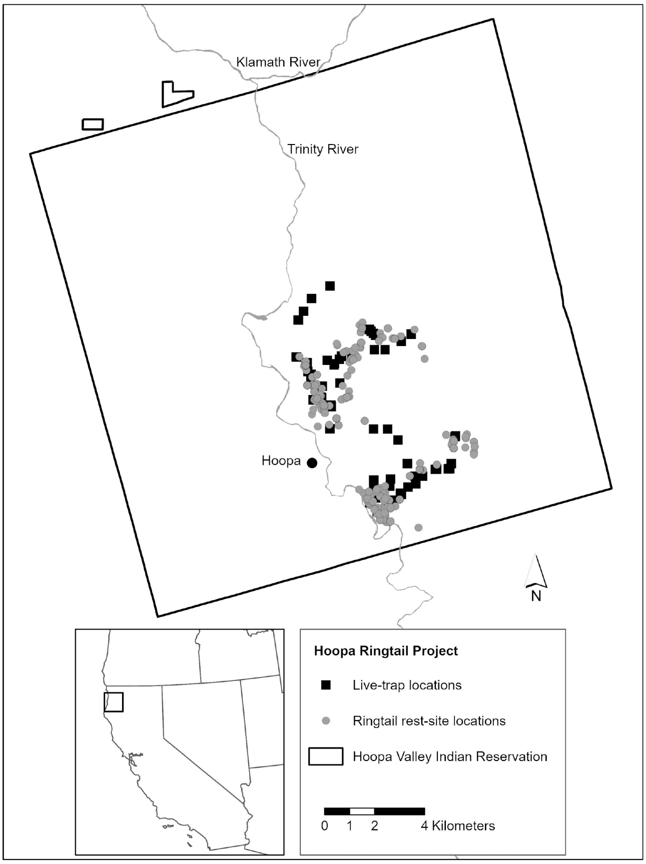

Figure 1. Locations where ringtails (*Bassariscus astutus*) were live-captured, radio collared, and re-located on the Hoopa Valley Indian Reservation (364 km^2) in northwestern California between 05 January and 13 August 2008.

Methods

Study Area

Our study occurred within the Hoopa Valley Indian Reservation (hereafter, "Hoopa"; Figure 1). Hoopa occupies 364 km^2 in northwestern California in eastern Humboldt County, with elevation range of 97 to 1,100 m asl (Singer and Begg 1975). Approximately 339 km^2 (93%) of Hoopa is forested and is dominated by Douglas-fir (*Pseudotsuga menzeii* (Mirb.) Franco), tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) P. S. Manos, C. H. Cannon, & S. H. Oh), and Pacific madrone (*Arbutus menziesii* Pursh). Non-forested areas (7%) include rural development, natural prairies, large rock outcrops, and brush fields, and are distributed throughout the forested landscape (Matthews 2012). The annual mean minimum and maximum monthly temperatures from 2008 to 2010 were 7.4 °C and 21.1 °C, respectively (Western Regional Climate Center 2019). Annual mean precipitation during the same period was 210 cm (Western Regional Climate Center 2019).

The forests of Hoopa are a mosaic of late- and early-seral conditions following a 60-year history of timber management (Baker 2003). Clearcuts were the predominant silvicultural treatments applied to 30% of Hoopa between 1960 and 1980 by the Department of Interior, Bureau of Indian Affairs. Since 1994, tribal forest managers have harvested an annual mean of 23,196 m^3 (9.83 million board feet of timber) on approximately 150 ha of forest, performed pre-commercial thinning on approximately 165 ha, removed competing brush from early-seral stands (i.e., early-release) on 100 to 175 ha, and burned for cultural-resource management on 6 to 40 ha, all under the direction of the Hoopa Tribe's Forest Management Plan (Hoopa Valley Tribe 2010). Harvest management occurs annually on small managed stands (< 10 ha) using an uneven-aged management system and regeneration methods with green tree (12 trees per ha > 50 cm DBH) and snag retention to perpetuate managed stands with at least three distinct tree age classes (10 to 29 years, 30 to 79 years, and ≥ 80 years).

Capture and Handling

We captured ringtails between December 2007 and March 2008 using Tomahawk live traps (models 102 and 108; Tomahawk Live Traps, Hazelhurst, WI), modified with plywood nest boxes to provide security, reduce environmental stress, and facilitate the handling of captured animals (Fowler and Golightly 1994, Gabriel and Wengert 2005). We distributed traps based on auxiliary detections of ringtails during an independent research project surveying for fishers using track plates and live traps (Matthews 2012). Traps were usually placed within 100 m of a drivable road for efficient access by observers. All captured ringtails were anesthetized with ketamine hydrochloride (25 mg kg^{-1}; Zoetis, Parsippany-Troy Hills, NJ) delivered by intramuscular injection. Adult ringtails, determined at capture (i.e., females weighing > 700 g and males weighing > 900 g; Callas 1987), were fitted with very-high-frequency (VHF) telemetry collars (Supply Two-Stage Transmitter, Sirtrack Wildlife Tracking Solution, Havelock North, New Zealand). Our capture and handling procedures were approved by Humboldt State University Institutional Animal Care and Use Committee (06/07.W.123-A).

Telemetry Data Collection

We located animals from 5 January through 13 August 2008 using a hand-held VHF receiver (R1000, Communications Specialists, Inc., Orange, CA) and a two-element Yagi antenna (RA-14, Telonics Inc., Mesa, AZ). The radio transmitters were equipped with an activity processor that indicated activity (40 pulses per minute [ppm]), inactivity (30 ppm after 5 seconds of inactivity), and mortality (80 ppm after 8 hours of inactivity). We followed inactivity signals to locate ringtails at rest sites and only tracked the same individual in bouts separated by > 18 hours (Myers 2010). Waiting > 18 hours allowed for nocturnal activity between relocations and independence between rest-site locations. We located rest sites by triangulating and homing until an individual tree or other structure was isolated and identified as the position of the collared ringtail. The structure's location was recorded using a hand-held global positioning system unit (Garmin GPSMAP 62ST; Garmin International, Inc., Olathe, KS) with a three-dimensional fix and an estimated error of ≤ 10 m. We attempted to locate each ringtail at a minimum of one rest site per week to distribute locations evenly throughout the study period.

Rest-Site Selection Variables

We used several habitat characteristics as predictor variables for ringtail rest-site selection. We first delineated forest stand categories that differed in age and relative amounts of mature trees, shrubs, and brush. Forest stand categories were: 1) mature forest dominated by mature trees, often with multiple canopy layers and downed wood; 2) stem-exclusion stage dominated by dense pole-size trees and little to no shrub cover; 3) oak woodland dominated by mature true oak trees (*Quercus* spp.) and little to no shrub cover; 4) young forest dominated by dense brush and sapling or pole-size trees; 5) brush dominated by a dense understory of young trees, shrubs, and herbs and little to no tree cover; and 6) open areas dominated by a non-forested condition (e.g., prairie, development, recent logging activity). Discrete forest stands were vector polygons classified based on the time since the last harvest and silvicultural treatment following Oliver and Larson (1996). We delineated forest stands as a 10-m grid cell raster layer using the 'raster' package (Hijmans 2019) and calculated the proportion of the stand types in each grid cell in R (R Core Team 2019). From these proportions, we classified each grid cell as the predominant stand type and used forest stand type as a categorical covariate. Distances to stand edge and water were calculated as the Euclidean distance between the rest site, the nearest stand edge, and the nearest perennial (i.e., year-round continuous flow of surface water) creek, represented as vector data.

Concurrent to our study of ringtail rest-site selection, another project studied fisher space use by collecting their locations using ground-based triangulations with radio telemetry following the methods of Matthews et al. (2011, 2013). Using the telemetry data that were a temporal match to the ringtail study, we estimated male and female fisher space use with a 95% fixed-kernel density estimator (Worton 1989). The fixed-kernel density estimates were obtained using the 'adehabitatHR' package (Calenge 2015) in R (R Core Team 2019); we used the reference bandwidth and discretized the density estimates into 30-m grid cells (Calenge 2015). We used the estimated value of the utilization distributions for males and females at each rest site as predictors for ringtail site selection. We used separate utilization distribution estimates for male and female fishers because we expected ringtails might associate higher levels of risk related to increased space use by male fishers compared to female fishers (McDonald et al. 2008, Remonti et al. 2012, Lesmeister et al. 2015).

Rest-Site Selection Model

We estimated rest-site selection with a used-available sampling framework (Boyce and McDonald 1999, Fortin et al. 2005, Fieberg et al. 2021). To determine potentially available rest-site locations, we calculated minimum convex polygons for each ringtail with ≥ 5 telemetry locations using the 'adehabitatHR' package in R (R Core Team 2019). We buffered each minimum convex polygon by 430 m (i.e., the mean radius of the minimum convex polygons) and placed 100 random locations within each combined minimum convex polygon and corresponding buffer (Northrup et al. 2013, Wattles et al. 2018). This definition of availability would correspond to third-order, or within-home-range, selection (Johnson 1980). We extracted habitat covariates at each rest-site location (available and used) using the 'raster' and 'rgeos' (Bivand and Rundel 2020) packages in R (R Core Team 2019).

We compared habitat covariates at rest sites with available locations within their home range using a weighted mixed-effects logistic regression, which was fit using the 'glmmTMB' package in R (Brooks et al. 2017, R Core Team 2019). When fit to a dataset collected under a used-available sampling design, the logistic regression model can describe relative probabilities of habitat use and is referred to as a resource selection function (Boyce and McDonald 1999, Fortin et al. 2005). We used a random intercept to account for repeated measures on individual ringtails and to account for the difference in available habitat among individuals (Gillies et al. 2006, Hebblewhite and Merrill 2008), but fixed the variance of the random intercept to a large value to avoid shrinking the individual-level intercepts to an overall mean (Muff et al. 2020). We assigned a weight of 1,000 to the available locations (used locations maintained a weight of 1), which allowed the likelihood of the logistic regression to converge to an inhomogeneous Poisson point process (Warton and Shepherd 2010, Muff et al. 2020). We fit a single model with all variables included as predictors (Table 1).

The effects of stand types were estimated relative to mature forests, characterized by stands dominated by mature trees, often with multiple can-

TABLE 1. Model covariates predicted to influence the selection of rest sites by ringtails (*Bassariscus astutus*) on the Hoopa Valley Indian Reservation in northwestern California. Forest stands were categorized based on tree age and species composition of each forest stand during the duration of the study (05 January and 13 August 2008) following Oliver and Larson (1996).

Covariate	Description
Mature forest	Forest stand dominated by hardwood and coniferous mature trees (frequently > 80 years old), often with multiple canopy layers and downed wood
Stem exclusion	Forest stand dominated by dense pole-size trees and little to no shrub cover
Oak woodland	Forest stand dominated by mature true oak (*Quercus* spp.) trees
Young forest	Forest stand dominated by dense brush and sapling or pole-size trees
Brush	Forest stand dominated by dense brush
Open	Area dominated by a non-forested condition (e.g., prairie, rural development, recent logging activity)
Distance to water	Distance to the nearest perennial stream or river
Distance to stand edge	Distance to the nearest stand edge, a transition from one forest class to another
Use by female fishers	Female fisher space use estimated as a 95% fixed-kernel density estimate of telemetry relocations
Use by male fishers	Male fisher space use estimated as a 95% fixed-kernel density estimate of telemetry relocations

opy layers and downed wood. Given that our categorical forest stand types were not equally represented within Hoopa (Figure 2), and the continuous environmental covariates may differ across stand types, we integrated the spatial utilization distribution over a given stand type compared to mature forest (the reference stand type). We followed the methods described by Fieberg et al. (2021) and divided the expected values on the real scale at the available points for a given stand type by the same for the available points in mature forest. The adjusted relative selection strength values for forest stand categories represent how much more likely an individual is to be found in a given habitat, accounting for the relative amounts of each type and the relationship between continuous variables, assuming the area within the buffered home range is equally available to them. All analyses were conducted using R Statistical Software v3.6.1 (R Core Team 2019).

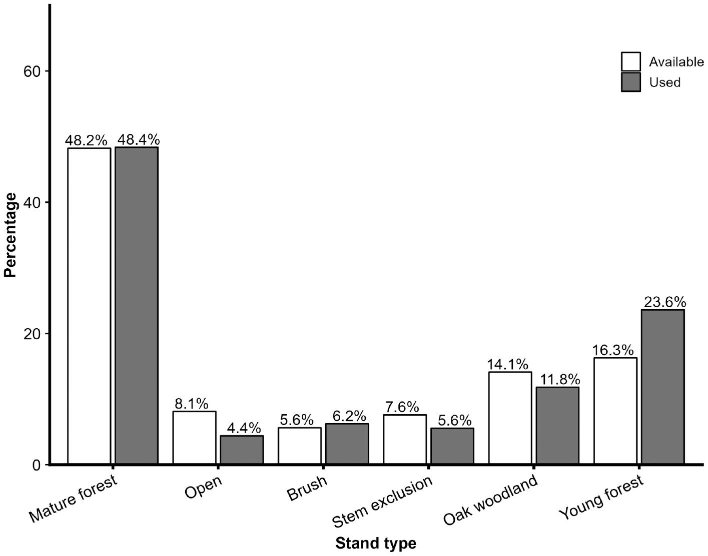

Figure 2. Distribution of the available and used locations among the different stand types for 16 ringtails (*Bassariscus astutus*) on the Hoopa Valley Indian Reservation in northwestern California between 05 January and 13 August 2008. Percentages were calculated by dividing the number of available and used locations in each stand type by the total number of available and used points in our analyses, respectively.

Results

We captured 24 ringtails (15 male, 9 female) and collared 16 (8 male, 8 female) on 52 occasions during 2,466 trap nights between 21 December 2007 and 27 March 2008. Only 16 ringtails were

TABLE 2. The frequency of use of forest structures and microsites of 140 unique rest sites used on 431 occasions by ringtails (*Bassariscus astutus*) between 05 January and 13 August 2008 on the Hoopa Valley Indian Reservation in northwestern California. Tree and snag species included California black oak (*Quercus kelloggii* Newberry), tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), Douglas-fir (*Pseudotsuga menziesii*), canyon live oak (*Quercus chrysolepis* Liebm.), white alder (*Alnus rhombifolia* Nutt.), and Oregon white oak (*Quercus garryana* Douglas ex Hook.).

Structure	Species	Microsite	Unique	Reuse
Live tree	California black oak	Tree cavity	22	67
		Broken top	1	6
	Tanoak	Tree cavity	16	31
		Broken top	1	1
		Large branch	1	2
	Pacific madrone	Tree cavity	16	29
	Douglas-fir	Tree cavity	3	38
		Broken top	1	2
		Bird nest	2	3
		Unknown	1	1
	Canyon live oak	Tree cavity	3	12
		Broken top	2	24
	White alder	Tree cavity	1	1
	Oregon white oak	Tree cavity	1	2
Snag	Douglas-fir	Tree cavity	11	88
		Broken top	6	25
	California black oak	Tree cavity	3	7
		Broken top	2	2
	Tanoak	Tree cavity	4	11
	Pacific madrone	Tree cavity	2	6
		Broken top	2	2
Rocky outcrop			16	25
Woodrat nest			11	12
On ground			4	4
Log			3	3
Slash pile			2	3
House or trailer			2	23
Stump			1	1

radio-collared due to limited resources and a desire for an equal sex ratio of monitored ringtails. We located ringtails on 431 occasions at 140 unique rest sites between 05 January and 13 August 2008. Most of the rest sites were in live trees (*n* = 71, 50.7%) and snags (*n* = 30, 21.4%; Table 2). Rest sites were most frequently in live California black oak (*Quercus kelloggii* Newberry) (*n* = 23, 16.4%), tanoak (*n* = 18, 12.9%), Douglas-fir snags (*n* = 17, 12.1%), and live Pacific madrone (*n* = 16, 11.4%; Table 2). Reused rest sites were most frequently in Douglas-fir snag cavities (*n* = 88, 20.4%) and cavities in live California black oak (*n* = 67, 15.5%; Table 2). Microsites for rest sites were most often tree cavities (*n* = 82, 58.6%) and the broken tops of trees (*n* = 15, 10.7%; Table 2).

We calculated the relative selection strength based on our coefficient estimates (Figure 3, Table 3) from the rest-site selection model and found that ringtails were 5.94 times more likely to choose a rest site in mature forest (the reference level) than open areas, and 3.42 times more likely to choose a rest site in mature forest than oak woodland. Compared to mature forest, there was no significant difference in relative selection strength among brush, stem exclusion, and young forest (Figure 3, Table 3). Ringtails were more likely to choose a rest site farther from a perennial water source than a site closer to water when all other predictors were held constant (Figure 3, Table 3). Ringtails were more likely to select a rest site closer to a stand-type edge than a location farther from an edge when all other environmental conditions were the same (Figure 3, Table 3). Fisher space use did not influence ringtail rest-site selection (Figure 3, Table 3).

Discussion

We found that in Douglas-fir-dominated forests managed for timber and cultural resources, ringtails were more likely to select rest sites in mature forest stands compared to other available habitats. Mature stands in Douglas-fir-dominated forests support a diverse assemblage of cavity-obligate species (Callas 1987, Michel and Winter

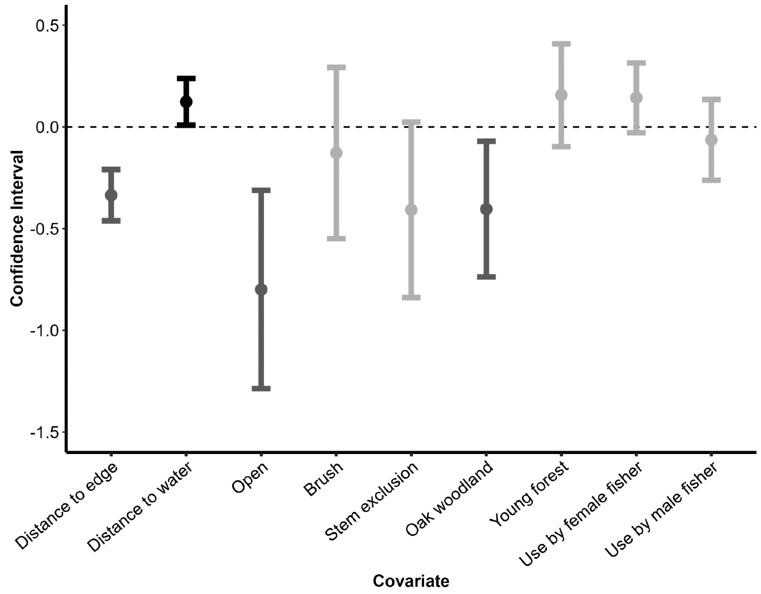

Figure 3. Estimates and 95% confidence intervals (CI) of fixed effects describing rest-site selection of ringtails (*Bassariscus astutus*) obtained using a mixed-effects logistic regression model. Effect sizes for categorical predictors are relative to the intercept (mature forest stands). A light gray 95% CI represents an interval that overlapped zero, a black 95% CI is a positive effect, and a dark gray 95% CI is a negative effect.

2009) and may provide the necessary resources (e.g., downed wood, hard and soft mast) to support ringtail energetic requirements (Chevalier 1989, 1992). Our findings indicated that ringtail rest-site selection in these forests may stem from a complex relationship among management history, food availability, and edges between forest patches with contrasting species composition and ages of dominant trees.

We found ringtails selected rest sites closer to stand edges. Although generally perceived as deleterious, edge habitat can provide a mosaic of resources for wildlife (Ries et al. 2017). Additionally, we found ringtails selected early-seral stands dominated by brush and stands dominated by dense brush and sapling or pole-size trees. We suspect these results, in conjunction with selecting rest sites closer to stand edges, are a function of the retention of trees and snags with wildlife value (e.g., cavities) during past logging operations (Hoopa Valley Tribal Council 2010), and the availability of potential food resources. Compared to late-seral forest stands, early-seral stands support high abundances of pinyon mouse (*Peromyscus truei*), dusky-footed wood rat (*Neotoma fuscipes*), and Allen's chipmunk (*Tamias senex*) (Whitaker 2003). These small mammal species are an important component of ringtail diets. For example, Alexander et al. (1994) found that 91% of ringtail fecal samples collected in southern Oregon contained animal material, with rodents making up the largest component of mammalian food items. Our understanding of species associated with late-seral or old-growth forest, such as fisher and California and northern spotted owl (*Strix* Xántus spp.), has evolved with emerging evidence that these species also utilize edges between patches of older and younger forests (Franklin et al. 2000, Raley et al. 2012, Sauder and Rachlow 2015). The importance of edge habitat for forest-obligate species has implications for future management strategies (Melin et al. 2018, Sellers et al. 2018), such as incorporating a matrix of stand ages to promote conservation of these species.

We also observed habitat selection relationships that are contrary to what has been reported in the literature (Trapp 1978, Toweill and Teer 1980, Poglayen-Neuwall and Toweill 1988, Yarchin 1994, Carroll 1997, Campbell 2004). Ringtails in Hoopa were less likely to select a rest site in oak woodlands compared to mature conifer-hardwood forests. We suspect that the available late-seral mixed conifer-hardwood stands in the Pacific Northwest provided ringtails with more abundant resources (e.g., rest sites, prey) and sufficient cover to avoid predation compared to oak woodlands. Oak woodlands in Hoopa are dominated by an overstory of mature true oaks (*Quercus* spp.)

TABLE 3. Estimates of fixed effects describing rest-site selection of ringtails (*Bassariscus astutus*) obtained using a weighted mixed-effects logistic regression model. Effect sizes for categorical predictors were relative to mature forest stands and are presented on the logit scale. Model estimates are presented on the logit scale and shaded values indicate significance at $P < 0.05$.

Predictors	Estimate	SE	95% CI	*P*-value
(Intercept)	0.00	242.54	–475.36 to 475.36	1.000
Open	–0.80	0.25	–1.29 to –0.31	0.001
Brush	–0.13	0.21	–0.55 to 0.29	0.550
Stem exclusion	–0.41	0.22	–0.84 to 0.02	0.064
Oak woodland	–0.40	0.17	–0.74 to –0.07	0.018
Young forest	0.16	0.13	–0.10 to 0.41	0.225
Distance to water	0.12	0.06	0.01 to 0.24	0.035
Distance to edge	–0.34	0.06	–0.46 to –0.21	< 0.001
Use by female fishers	0.14	0.09	–0.03 to 0.31	0.102
Use by male fishers	–0.06	0.10	–0.26 to 0.13	0.529

and little to no understory cover (Jimerson and Carothers 2002). Additionally, ringtails were less likely to select rest sites in close proximity to perennial water sources in Hoopa. While Trapp (1978), Richards (1976), Toweill and Teer (1980), and Yarchin (1994) located ringtails near water or riparian areas, these differences in ringtail selection may be a function of greater perennial water availability in Hoopa compared to more arid environments in the southwestern United States. More research focusing on ringtail habitat use and selection should be conducted, as our work focused on a small portion of their range periphery with a small sample size. However, these results highlight how habitat selection by ringtails might differ in northern, forested portions of their range compared to southern, more arid areas of their range (Davies et al. 2013, Holbrook et al. 2017).

Ringtails and fishers occupy similar forest conditions and utilize similar forest resources in Hoopa (Yaeger 2005, Myers 2010). Ecological theory suggests that subordinate species often modify their realized niches by altering habitat selection (St-Pierre et al. 2006). Thus, we hypothesized that the selection of rest sites by ringtails might be influenced by fishers due to interference competition for rest sites or to predation pressure. Despite the potential for this, the intensity of space use by male or female fishers did not affect the selection of rest sites by ringtails. It is important to note that the male and female fisher utilization distributions represent relative space use across the landscape and was not focused on fisher rest-site selection. Therefore, there may be low levels of competition associated with diurnal rest sites located within fisher habitat that we could not elucidate in our study. In contrast, our ringtail analysis was performed at a much finer selection scale (i.e., rest site). Fishers may exhibit competitive pressure on ringtails and influence their selection choices during other activities beyond diurnal rest-site selection (McGarigal et al. 2016), as ringtails and fishers overlap in range, diet, and habitat requirements (McDonald et al. 2008, Remonti et al. 2012, Lesmeister et al. 2015). While we did not detect an effect of fisher space use on ringtail rest-site selection, this could be due to temporal partitioning, as fishers are more crepuscular (McCann et al. 2019) and ringtails are more nocturnal (Kavanau 1971). Further studies of interactions between members of the mesocarnivoran guild should be conducted to improve our understanding of these relationships.

Ringtails most frequently selected tree cavities as rest sites (Table 2). A majority of cavities were found in live California black oak, tanoak, and Pacific madrone, and in Douglas-fir snags and live trees. The development of cavities and other microsites used by secondary-cavity obligates occurs under specific conditions over decades of stand development (Edworthy and Martin 2013, 2014). Mature stands in Hoopa were of sufficient age and species composition that provided conditions capable of promoting cavity genesis and development (Franklin et al. 2002, Blake 2018). The conservation of existing microsites and maintaining the natural processes of tree growth, damage, disease, and decay that allow for the development of microsites are important for conserving ringtails and co-occurring secondary cavity obligate species (Bull 2002, Weir et al. 2012).

Uneven-aged forest management, live-tree and snag retention targets, and distribution of late- and early-seral forest conditions on Hoopa provided suitable conditions in several stand types for diurnal rest-site selection by ringtails. We suspect ringtails exhibit similar selection patterns in other areas of Douglas-fir-dominated forest in the northern portions of their range. These selection patterns offer guidance for forest management throughout Hoopa and neighboring forests. The uneven-aged management system and regeneration methods applied under the Hoopa Tribe Forest Management Plan provided forest conditions, and therefore potential structures, suitable for diurnal rest sites throughout Hoopa (Hoopa Valley Tribal Council 2010). Although our study was focused on Hoopa, similar uneven-aged management systems informed by traditional tribal perspectives occur on other tribal forests and US Forest Service land (Charnley et al. 2014, Long and Lake 2018, Long et al. 2020). These similar practices provide management opportunities for conserving and recruiting forest conditions used by ringtails for diurnal rest sites. Future research into ringtail habitat selection should evaluate selection patterns at different spatial scales, recognizing the importance of other forest resources required by ringtails (Lawler and Edwards 2006). Our study, which focused on understanding the forest stand-level characteristics of rest-site selection by ringtails on the periphery of their range, is an important step in determining optimal forest management actions to aid in their conservation (Bunnell 2013) and provides a strong foundation to ask further questions regarding ringtail microsite selection.

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