



Reproductive den selection and its consequences for fisher neonates, a cavity-obligate mustelid

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Selection of habitat characteristics by reproductive females during neonate development can mediate the influence of adverse environmental conditions on the fitness of offspring. Previous research has suggested that cavities and burrows used for reproduction by cavity-obligate species offer thermoregulatory benefits, access to prey, and can limit predation pressure. As fishers (*Pekania pennanti*) are secondary cavity-obligate breeders, we hypothesized that they select particular characteristics of reproductive den cavities at discrete stages of offspring development to mediate adverse biotic and environmental effects on their neonates. To test our hypothesis, we located 406 reproductive dens and 154 cavity rest sites used by 65 individual adult female fishers during 11 reproductive seasons (2005–2016) in northwestern California. We counted 53 (27 F, 26 M) kits in 31 litters born to 19 females during six of these reproductive seasons. The weight of kits varied significantly by sex and by age, whereas the length of kits varied only by age, suggesting that adult females in this population might be preferentially investing in male kits. We found that natal and early-maternal dens buffered minimum temperatures significantly more than late-maternal dens and cavities used during the nonreproductive season. A male fisher skull was also less likely to fit through the cavity openings of natal dens than through the openings of cavities used by adult females during the nonreproductive season. Litter survival was significantly lower at natal dens than at late-maternal dens. The age of adult female fishers did not affect the probability of litter survival. Our results emphasize the vulnerability of vertebrate offspring during early developmental periods and how cavity-obligate species select cavities to mediate environmental conditions during reproduction.

Key words: cavity-obligate, fisher, neonate, *Pekania pennanti*, reproduction, reproductive den selection

Environmental conditions during early development can affect survival and fecundity of individuals, influence population dynamics, and optimize life histories (Lindström 1999; Monaghan 2008; Garratt et al. 2015; Marshall et al. 2017). A diverse range of taxa use confined spaces (e.g., tree cavities, underground burrows) to mediate the effects of biotic and environmental conditions on their offspring and to increase reproductive success. For example, tree cavities can provide more stable microclimates than ambient conditions, maintain higher temperatures during cold nights, and provide for energy savings

for New Zealand long-tailed bats (*Chalinolobus tuberculatus*—Sedgeley 2001). Cavities can also limit the effects of predators and nest-site competitors; nest survival for nuthatches (*Sitta europaea*), blue tits (*Cyanistes caeruleus*), Lewis's woodpeckers (*Melanerpes lewis*), and a community of cavity-nesting birds in northeastern Argentina was found to be greater in cavities with smaller entrance diameters (Wesołowski and Rowiński 2004, 2012; Zhu et al. 2012; Cockle et al. 2015). Generally, offspring survival can decline in areas without enough suitable sites for reproduction (Anderson et al. 1976; Cockle et al. 2010), and this

in turn has negative consequences for population trajectories (Newton 1994; Gibbons and Lindenmayer 2002; Cockle et al. 2011, 2015; Bunnell 2013). Thus, it is important to determine the links between the selection of sites used for reproduction and neonate survival.

The fisher (*Pekania pennanti*) is a medium-sized, forest-obligate carnivore of conservation concern in the U.S. Pacific states (U.S. Fish and Wildlife Service 2014, 2016a). Female fishers are secondary-cavity-obligate breeders, thereby relying on physical damage, fungal decay, or primary cavity excavators (e.g., pileated woodpeckers [*Dryocopus pileatus*]) for the creation of cavities (Lofroth et al. 2010; Raley et al. 2012; Green et al. 2018). Female fishers birth and raise kits in cavities in large-diameter, live, and standing-dead trees (i.e., snags; Lofroth et al. 2010; Raley et al. 2012; Zhao et al. 2012; Green et al. 2018). Fishers are among the largest tree-cavity users in North America, selecting reproductive dens with specific features occurring in a narrow range of tree species and sizes (Lofroth et al. 2010; Raley et al. 2012; Weir et al. 2012; U.S. Fish and Wildlife Service 2016b; Green 2017). Female fishers have been documented to use up to seven reproductive dens during a single reproductive season (Paragi 1990; Matthews et al. 2013; Green et al. 2017), consisting of a natal den (the reproductive den where parturition occurs) and up to six subsequent maternal dens (any reproductive den used subsequent to the natal den—Lofroth et al. 2010; Green et al. 2017). The selection of reproductive den sites by fishers should have positive effects on kit development and survival, given the effort it takes to relocate so often.

Fisher kits are particularly vulnerable to mortality (Matthews et al. 2013; Sweitzer et al. 2016; Green 2017), and what little is known of early, postpartum development mostly comes from captive studies (Coulter 1966; LaBarge et al. 1990; Powell 1993; Frost and Krohn 2004). Frost and Krohn (2004) reported that kits born in captivity were altricial from birth to 6 weeks. Tooth eruption, the opening of eyelids and ear canals, and maternal provisioning of solid food were reported to occur between 40 and 50 days postpartum (Coulter 1966; LaBarge et al. 1990; Powell 1993; Frost and Krohn 2004). Growth of kits increased rapidly following the opening of eyelids and ear canals and sexual dimorphism was apparent by 60 days postpartum (Frost and Krohn 2004). By 70 days postpartum, kits left the nest box and moved around in cages unassisted (Frost and Krohn 2004). Similarly, Paragi et al. (1996) reported that wild female fishers in Maine used reproductive dens an average of 71 days (range 58–80 days), leading Frost and Krohn (2004) to conclude that fisher kits they raised in captivity developed at rates similar to kits in the wild.

Female fishers give birth to an average of 1.9 kits in a single litter per year in the Pacific states (Green et al. 2018) and kit mortality during early development is likely very high. In captivity, Frost and Krohn (2004) reported 26.3% of kits died within the first 7 days postpartum. In the wild, the percentage of litters that did not survive to weaning has been documented to range between 15% and 60% (Matthews et al. 2013; Green et al. 2018). These estimates from wild populations do not

include known and unknown instances where individual kits died but siblings persisted to weaning, likely resulting in an underestimate of kit mortality. Thus, the ecological conditions in early life and reproductive den selection by females may be particularly important for kit survival.

Adult female fishers likely select reproductive dens to maximize offspring survival, although this has rarely been tested. Fishers are hypothesized to select reproductive dens that provide shelter for females and kits from inclement weather, access to prey, protection from predators (e.g., mountain lions [*Puma concolor*], bobcats [*Lynx rufus*]), and restrict male fishers seeking breeding opportunities from accessing the interior of the reproductive den cavity (Lofroth et al. 2010; Weir et al. 2012; Green et al. 2018). Previous research has offered initial insights into the selection of reproductive dens by female fishers (Paragi et al. 1996; Powell et al. 1997; Green 2017), but no one has empirically tested the relationship between selection of reproductive dens and the stages of postpartum development or survival of offspring (Lofroth et al. 2010; Raley et al. 2012).

Here, we investigated the interactions among kit development, reproductive den characteristics, and kit survival. We first evaluated relationships between kit weight and body length during early kit development and tested for differences between sexes. Next, we defined six a priori hypotheses proposing explanations for differences among reproductive dens and cavity rest sites used during the nonreproductive season. We divided reproductive dens into three classes based on developmental patterns of kits observed during captive rearing. Tooth eruption, opening of eyes and ear canals, awkward crawling, and the provisioning with solid food begin as early as 40 days postpartum (Coulter 1966; LaBarge et al. 1990; Powell 1993; Frost and Krohn 2004). Thus, we classified reproductive dens as 1) natal (where parturition took place), 2) early maternal (any reproductive den selected after the natal den and up to 40 days postpartum), and 3) late maternal (any reproductive den selected >40 days postpartum). We defined a cavity rest site as cavity microsite in the bole of a tree or snag where an individual animal was located during a period of inactivity in the nonreproductive season (Kilpatrick and Rego 1994; Zielinski et al. 2004b; Aubry et al. 2018). We did not divide cavity rest sites into subcategories.

Recognizing that fishers select habitat features at different spatial scales (Weir and Harestad 2003; Raley et al. 2012; Green 2017), our hypotheses included variables measured at the forest stand, patch, and microsite scales (Johnson 1980; Lofroth 1993). Specifically, we investigated differences between natal dens and later-season reproductive dens and cavities used in the nonreproductive season in 1) whether they were located in stands of mature forest, 2) their proximity to stands with high prey abundance, 3) whether they provided opportunities to escape predators in the patch around the reproductive den or rest site, 4) the likelihood that a male fisher seeking a breeding opportunity could fit through the cavity opening of the microsite, 5) the capacity of the microsite to buffer minimum temperatures, and 6) the capacity of the microsite to buffer maximum temperatures. We then investigated

differences in litter survival across developmental stages to weaning, and investigated how litter survival was influenced by maternal age.

MATERIALS AND METHODS

Study area.—Our study area was located on the Hoopa Indian Valley Reservation (henceforth, Hoopa) in north-western California. Mean daily minimum, average, and maximum temperatures were 6°C, 14°C, and 23°C, respectively, and mean annual precipitation, primarily in the form of rain, was 141 cm (National Centers for Environmental Information 2018). The dominant land cover types on Hoopa were forests with an overstory of Douglas-fir (*Pseudotsuga menziesii*) and a mid-story of tanoak (*Notholithocarpus densiflorus*), madrone (*Arbutus menziesii*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), and canyon live oak (*Q. chrysolepis*). Mountain lions and bobcats were the dominant fisher predators (Wengert et al. 2014; Gabriel et al. 2015) and dusky-footed woodrats (*Neotoma fuscipes*), *Peromyscus* spp., and western gray squirrels (*Sciurus griseus*) were the dominant fisher prey (Golightly et al. 2006; Slauson et al. 2011). Fishers are culturally significant to the Hoopa Tribe and they are only harvested on rare occasions for ceremonial regalia (Cooperrider et al. 2000).

A 60-year history of forest management in Hoopa created a mosaic of mature old-growth and early seral forests. The Bureau of Indian Affairs managed timber resources in Hoopa between 1960 and 1980. Clearcuts were the predominant silvicultural practice applied to 30% of Hoopa. An average of 500 ha was cut per year across multiple clearcuts averaging 19 ha, although cuts up to 276 ha occurred. Between 1994 and 2010, tribal forest managers harvested 23,196 m³ (9.83 million board feet) annually on approximately 150 ha, pre-commercially thinned approximately 165 ha, early-released 100–175 ha, and burned 6–40 ha for cultural resource management, all under the direction of the Hoopa Tribe's Forest Management Plan. Harvest was implemented using regeneration methods with green tree (12 trees/ha > 50 cm diameter at breast height) and snag (all that do not pose a safety hazard) retention in small (< 10 ha) stands. A minor amount of commercial thinning and single-tree and group selection was also employed.

Capture and marking of fishers.—We captured fishers annually from September through February between 2005 and 2016 using cage-type live traps (model 207, Tomahawk Live Trap Company, Tomahawk, Wisconsin) baited with chicken and modified with a plywood cubby box (Wilbert 1992; Seglund 1995). We anesthetized captured fishers with ketamine hydrochloride (40 mg/kg) and diazepam or midazolam (0.25 mg/kg). We fit female fishers > 1 year old (age estimated by body size and tooth wear) with VHF radio collars (Holohil model MI-2, Holohil Systems Ltd., Carp, Ontario, Canada or Telonics model MOD80, Telonics Inc., Mesa, Arizona). We removed a single tooth (P1) for estimating birth-year from cementum annuli (Matson's Laboratory, Milltown, Montana—Arthur et al. 1992). We released all fishers at their site of capture after

they had recovered for approximately 1 h and showed no visible signs of anesthesia. Our research methods adhered to the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and were approved by the Institutional Animal Care and Use Committee of Humboldt State University, protocol 04104.W.42.A.

Locating reproductive dens and tree cavities used by fishers.—Fishers use a wide range of forest structures during daily resting bouts (Zielinski et al. 2004b; Lofroth et al. 2010; Aubry et al. 2013). We used ground-based radiotelemetry to estimate locations of fishers and to identify reproductive dens and rest sites. Although fishers may rest in a variety of structure types (Kilpatrick and Rego 1994; Zielinski et al. 2004b; Aubry et al. 2018), for the purposes of our comparison with reproductive den sites, we focused on rest sites in live trees and snags with cavities. Locations of inactive fishers were obtained by hiking to the source of the VHF signal in the field (Springer 1979) following methods outlined by Matthews et al. (2013).

We attempted to locate inactive female fishers 3 to 5 days per week to observe use of sites during the early reproductive season each year (1 March to 15 April) as an indication of reproductive den establishment. Denning behavior was identified by a sudden change in activity from using numerous rest sites per week across a female's home range to movements restricted to a small portion of the female's home range and repeated use of the same structure while inactive. We defined the first day a female was observed using a natal den as the date of parturition. We located females an average of 3.6 ($SD = 1.4$) times per week during the reproductive season to document reproductive den abandonment and the establishment of new reproductive dens or failure to raise kits to weaning.

Early development of kits.—We climbed occupied reproductive den trees to measure kits between 17 and 67 days postpartum following methods outlined by Matthews et al. (2013). Briefly, we climbed reproductive den trees while the mothers were away using a single-rope technique or tree-climbing spurs and a flip rope (Jepson 2000). We determined the presence and number of kits visually, often with the aid of a Burrow Camera System (Sandpiper Technologies, Inc., Manteca, California). We then extracted kits from reproductive dens without altering the den structure. We weighed kits in grams in a nylon mesh bag with a Pesola Macro-Line Spring Scale (Schindellegi, Switzerland) and measured length in centimeter along the body contour from the tip of the nose to the base of the tail along the backbone. Kits were out of the den for a maximum of 60 min. We placed kits back in the reproductive den after all measurements were taken. We closely monitored the adult female for 2–3 days following kit extraction to assess the possibility of reproductive den or litter abandonment due to disturbance caused by us. We monitored behavior of adult females throughout the reproductive season to determine if the litter survived at each reproductive den cavity. The cavity was defined as successful if one or more kits were alive following a move to a subsequent reproductive den cavity or if one or more kits from this litter survived to an estimated average weaning date of 31 May (Powell 1993; Matthews et al. 2013).

We considered the final reproductive den to be unsuccessful if an adult female died prior to weaning her kits.

Vegetation data collection.—We collected vegetation data at the forest stand, patch, and microsite scales to evaluate our hypotheses about how natal dens differed from later-season reproductive dens and cavities used in the nonreproductive season. At the stand scale, we determined whether each reproductive den and rest site was located in a stand of mature forest and measured their proximity to stands with high prey abundance. Personnel from Hoopa Tribal Forestry classified discrete forest stands on Hoopa based on the time since last harvest and silvicultural treatment following [Oliver and Larson \(1996\)](#). Mature forest stands were dominated by multi- or single-storied forest ≥ 80 years old or younger forest conditions (46–79 years old) with closed canopy and residual mature structures. Mature forest was coded as a binary variable indicating whether the reproductive den or cavity rest site was located in a forest stand with the characteristics expected to support the structures and microsites (i.e., cavities) used by fishers. Forest stands with low canopy cover, moderate total cover, and high shrub cover were found to support high abundances of potential fisher prey in Hoopa, including *N. fuscipes*, *Tamias senex*, and *Peromyscus truei* ([Whitaker 2003](#)). In particular, [Whitaker \(2003\)](#) found the relative abundances of *N. fuscipes*, a dominant component of fisher diet ([Golightly et al. 2006](#); [Slauson et al. 2011](#)), were an order of magnitude greater in 20–25 years old, unthinned forest stands than in thinned stands of the same age or stands 35–40 years old regardless of thinning. Thus, we used these stands as a surrogate for areas of high prey abundance. We calculated the proximity of the reproductive den to stands with these characteristics using ArcGIS 10.3 (Environmental Systems Research Institute, Redlands, California).

At the patch scale, we estimated total basal area (m^2/ha) within a circular plot of 16 m radius centered on the reproductive den or rest site structure as a metric for the patch to provide opportunities in the form of vertical forest structure to escape predators. Fishers consistently select resting sites that have larger-diameter trees that may benefit fishers by providing protection from predators and secure sites for consuming prey ([Raley et al. 2012](#); [Aubry et al. 2013](#)). Given that survival rates of female fishers in populations not trapped for fur are lower during periods when they are caring for dependent young ([Higley et al. 2014](#); [Sweitzer et al. 2016](#)), and the leading source of mortality is predation ([Wengert et al. 2014](#); [Gabriel et al. 2015](#)), we hypothesized that female fishers might select den sites in forest patches with larger basal areas to escape predators.

At the microsite scale (i.e., the reproductive den cavity itself—[Aubry et al. 2018](#)), we evaluated the likelihood that a male fisher could fit through the cavity opening and the capacity of the microsite to buffer minimum and maximum temperatures by climbing a subset of reproductive dens and rest sites. Fishers mate within 10 days postpartum, decoupling breeding and parturition through delayed implantation ([Hall 1942](#); [Enders and Pearson 1943](#)). We hypothesized that risks associated with predation and behaviors of adult male fishers during the mating period could influence reproductive den selection by female

fishers (e.g., repeated attempts to mate, trampling, or suffocation of kits during mating). We, therefore, predicted that females select reproductive den cavities that prevented access by male fishers. We built a cast of a male fisher skull using plaster and paraffin wax, using mean zygomatic arch width (70 mm) measurements taken during live-capture and handling efforts on Hoopa. We tested whether this cast and, thus, a male fisher, could fit through the cavity opening (“skull fit”).

We measured the capacity of the reproductive den cavities to buffer minimum and maximum temperatures using HOBO Pendant Temp–Light Loggers (model UA-002-08; Onset Computer Corporation, Pocasset, Massachusetts). We predicted that females selected den cavities that provided more stable microclimates than ambient conditions, buffering minimum nighttime ambient temperatures particularly early in den season and buffering maximum daytime ambient temperatures particularly late in the den season. We deployed one logger inside the cavity on the cavity floor and a second logger outside the cavity level with the cavity floor on the south-southwest-facing side of the tree using Velcro tape (Paddington, London, United Kingdom) attached to the bark with nylon drywall anchors (Toggler SnapSkru, Norwalk, Connecticut). Loggers collected data between the average local parturition date (22 March—[Matthews et al. 2013](#)) and the estimated date of weaning (31 May—[Powell 1993](#)) in the year following use by a female fisher. Temperature buffering for each reproductive den cavity was defined as the difference between the outside temperature and the temperature within a tree cavity, and was calculated for both daily minimum and maximum temperatures. Due to accessibility and safety concerns, we climbed a larger proportion of live tanoak trees and lower proportions of live Douglas-fir trees and snags than fishers used.

Statistical analyses.—We used generalized linear mixed-effects models to investigate how kit weight and length varied by sex and age of the kit. We coded these models as:

$$\begin{aligned} \text{Kit weight or kit length} &\sim \alpha_0 [\text{mother identity}] \\ &+ \alpha_1 \times \text{sex} + \alpha_2 \times \text{age}, \end{aligned}$$

where the measured weight or length of each fisher kit was modeled to be a function of the identity of its mother coded as a random effect on the intercept (α_0), its sex (α_1), and its age in days (α_2). Age was standardized to have a mean of 0 and a *SD* of 1 for analyses.

We then used generalized linear mixed-effects models to investigate the differences among reproductive dens and cavity rest sites as a function of kit developmental stage. We tested our hypotheses to evaluate suspected differences between reproductive dens and cavity rest sites to exemplify what fishers selected during postpartum development. Specifically, we investigated if six different characteristics (presence of mature forest, proximity to stands with high prey abundance, basal area, male fisher skull fit, minimum temperature buffer, and maximum temperature buffer) varied among four different categorical variables (natal dens, early-maternal dens, late-maternal dens, and cavity rest sites). For each hypothesis, we coded the model as:

$$\begin{aligned} \text{Reproductive den characteristic} \sim & \\ & \alpha_0 [\text{female fisher identity (natal den)}] \\ & + \alpha_1 \times \text{early maternal} + \alpha_2 \times \text{late maternal} \\ & + \alpha_3 \times \text{rest site}, \end{aligned}$$

where the reproductive den characteristic of interest was modeled as an effect of the binary variables indicating whether this was an early-maternal den (α_1), a late-maternal den (α_2), or a rest site (α_3). We coded natal dens as the intercept and identity of female fishers as a random effect on the intercept in all models.

We also investigated if litter survival at each reproductive den cavity varied by stage of postpartum development and adult female age. We coded this model as:

$$\begin{aligned} \text{Success at reproductive den} \sim & \\ & \alpha_0 [\text{female fisher identity (natal den)}] + \alpha_1 \\ & \times \text{early maternal} + \alpha_2 \times \text{late maternal} + \alpha_3 \times \text{age}, \end{aligned}$$

where the binary variable indicating whether at least one kit in a litter survived at this reproductive den was modeled as a function of the binary variables indicating whether this was an early-maternal den (α_1) or a late-maternal den (α_2), and the adult female's age in years (α_3). Here, again, we coded natal dens as the intercept, and allowed this to vary by identity of female fishers. Age of females was standardized to have a mean of 0 and a *SD* of 1 for analyses.

We fit our models using the Markov chain Monte Carlo (MCMC) methods of JAGS (Plummer 2003) with the jagsUI package (Kellner 2016) in R v. 3.2.3 (R Core Team 2016). We used uninformative prior distributions for all parameters. Parameter estimates were calculated from 4,500 MCMC samples, taken from three chains run for 150,000 iterations, thinned by 100, following an adaptation and burn-in period of 100,000. We assessed model convergence by examining trace plots and $\hat{R}$ values for parameter estimates (Gelman and Hill 2007; Gelman et al. 2013). We evaluated model fit by calculating a Bayesian *P*-value. Although each model was run with a random effect of identity of adult female fishers on the intercept, we present all results as the mean intercept. We also present all results as mean (*SD*; 95% credible interval, *CI*). Parameters for which the 95% *CI* did not overlap zero were considered to be statistically significant.

RESULTS

We captured and radiomarked 85 female fishers estimated to be > 1 year old on 227 trap nights between 2004 and 2016. We monitored 65 female fishers of breeding-age (> 2 years old) over 11 reproductive seasons (2005–2016) on 189 denning opportunities. We monitored individual females for an average of 2.9 reproductive seasons (range 1–8) and females were 5 years old on average (range 2–11). Nine adult females died after giving birth but prior to weaning kits. We located 406 reproductive dens in 341 unique structures and 154 cavity rest sites in 134 unique structures (Table 1). Two dens were used on four independent occasions. One of these dens was used by a single female in four different years. The other den used on four occasions was used by two different females in four different years. Two rest sites were also used on four independent occasions. Most reproductive dens (47%) and cavity rest sites (37%) were in live tanoak trees (Supplementary Data SD1). Other species representing > 5% of the cavities used included California black oak (*Q. kelloggii*; 11%), giant chinquapin (*Chrysopsis chrysophylla*; 7%), and Douglas-fir (24%). The DBH (diameter at breast height) of conifers and hardwoods used averaged (*SD*) 115 (36) and 82 (23) cm, respectively (Supplementary Data SD2).

We counted 53 kits (27 F, 26 M) in 31 litters born to 19 females during six reproductive seasons (2005–2008, 2010, and 2014). We did not observe signs of a female fisher abandoning her litter after we handled their kits. Females moved their litters to a new reproductive den an average (*SD*) of 7 (10) days after handling their kits. The weight of kits (g) varied significantly by sex and by age; males were heavier than females and the weight of both sexes increased as the kits grew older (mean intercept = 335.62, *SD* = 28.14; *CI* = 272.87, 399.45; sex effect = 46.29, *SD* = 17.57, *CI* = 10.13, 80.24; age effect = 108.94, *SD* = 10.07, *CI* = 89.39, 128.56; Fig. 1). The length of kits (cm) varied significantly by age (intercept = 23.13, *SD* = 0.79, *CI* = 20.75, 25.51; age effect = 2.97, *SD* = 0.39, *CI* = 2.21, 3.74), but not by sex (sex effect = 1.33, *SD* = 0.71, *CI* = -0.12, 2.69; Fig. 1).

The skull of a male fisher was less likely to fit through the cavity openings of natal dens than cavity openings at rest sites (Table 2; Fig. 2). The cavity openings of early- and late-maternal dens were not significantly different from those of natal dens.

Table 1.—Reproductive dens and cavity rest sites selected by 65 individual adult female fishers (*Pekania pennanti*) over 11 reproductive seasons (2005–2016) for a total of 189 denning opportunities on the Hoopa Valley Indian Reservation in northwestern California. Reproductive den classes included natal (where parturition took place), early maternal (any reproductive den selected after the natal den and up to 40 days postpartum), and late maternal (any reproductive den selected >40 days postpartum). Cavity rest sites were not divided into subcategories. We present total sample sizes (*n*) that includes reuse of individual structures, the number of individual structures, and the number of reproductive dens and rest sites we sampled for each characteristic.

	Natal dens	Early-maternal dens	Late-maternal dens	Cavity rest sites
<i>n</i>	147	173	86	154
Individual structures	130	160	84	134
Mature forest and distance to prey	147	173	86	154
Basal area	65	79	32	84
Skull fit	52	56	16	47
Minimum and maximum temperature buffer	29	28	12	33

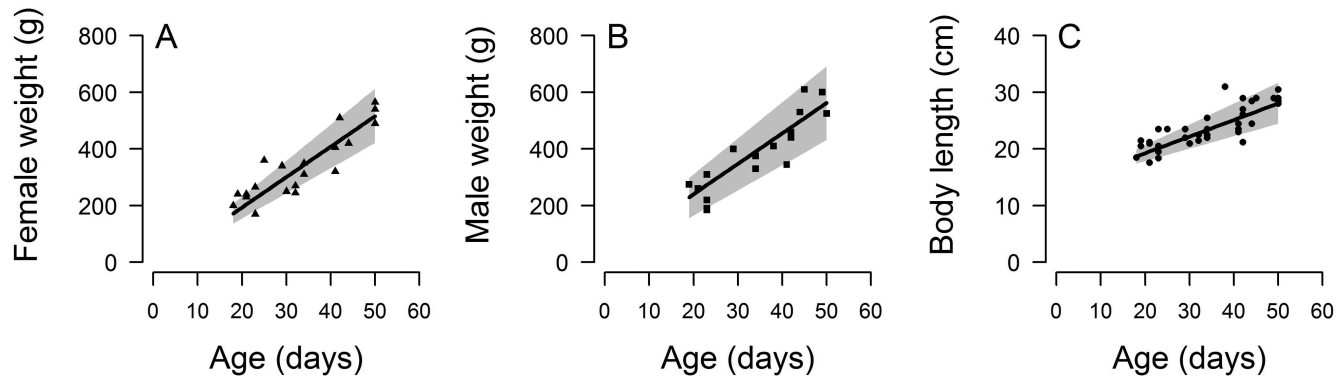


Fig. 1.—Differences in the weight of female (A; $n = 27$) and male (B; $n = 26$) fisher kits (*Pekania pennanti*) and variation in the length of female and male fisher kits (C) over the reproductive season on the Hoopa Valley Indian Reservation in northwestern California between 2006 and 2014. Both sex and age had significant effects on weight of kits (95% CI of the effect did not overlap zero). Length of kits did not vary by sex, but did vary significantly by age of the kit (95% CI of the effect did not overlap zero). The solid lines indicate the median posterior parameter effect size and the shading indicates the 95% CI around this effect. Triangles (A) represent a measurement of female kit weight, squares (B) represent a measurement of male kit weight, and circles (C) represent a measurement of kit length.

Table 2.—Results from the generalized linear mixed-effects models investigating differences in characteristics of fisher (*Pekania pennanti*) reproductive dens and rest site cavities by kit developmental period on the Hoopa Indian Valley Reservation in northern California between 2005 and 2016. Female identity was coded as a random effect in these analyses, but we present the average for all females here. Natal den cavities were coded as the intercept for all models. We present all results on the normal scale. Significant differences (parameter estimates 95% CI non-overlapping 0) are indicated in bold.

Parameter	Mean	SD	95% CI		
			2.5	50	97.5
Mature forest (%)					
α_0 (mean natal)	0.88	0.56	0.82	0.88	0.92
α_1 (early den)	0.03	0.08	−0.05	0.03	0.05
α_2 (late den)	0.03	0.1	−0.08	0.03	0.05
α_3 (rest site)	−0.06	0.08	−0.22	−0.06	0.02
Distance to prey habitat (m)					
α_0 (mean natal)	0.03	0.61	0.01	0.03	0.06
α_1 (early den)	0	0.09	0	0	0.07
α_2 (late den)	0.01	0.11	0	0.01	0.11
α_3 (rest site)	−0.01	0.11	−0.01	−0.01	0.05
Basal area (m ² /ha)					
α_0 (mean natal)	163.76	18.87	126.35	163.56	201.97
α_1 (early den)	−0.09	1	−2.05	−0.1	1.86
α_2 (late den)	−0.06	1.01	−2.09	−0.05	1.89
α_3 (rest site)	0.09	0.99	−1.84	0.08	2.03
Male fisher skull fit (%)					
α_0 (mean natal)	0.48	0.57	0.35	0.48	0.62
α_1 (early den)	0.14	0.09	−0.04	0.14	0.24
α_2 (late den)	0.24	0.13	0	0.24	0.31
α_3 (rest site)	0.29	0.1	0.11	0.29	0.31
Minimum temp buffer (°C)					
α_0 (mean natal)	2.63	0.18	2.27	2.63	2.97
α_1 (early den)	−0.43	0.24	−0.91	−0.43	0.05
α_2 (late den)	−0.81	0.32	−1.42	−0.81	−0.17
α_3 (rest site)	−0.57	0.24	−1.03	−0.57	−0.1
Maximum temp buffer (°C)					
α_0 (mean natal)	6.77	0.78	5.17	6.75	8.39
α_1 (early den)	−0.22	0.57	−1.34	−0.21	0.85
α_2 (late den)	−0.53	0.67	−1.85	−0.54	0.79
α_3 (rest site)	−0.63	0.56	−1.72	−0.63	0.47

Natal dens buffered minimum temperatures significantly better than late-maternal dens and cavity rest sites (Table 2; Fig. 2), but natal dens were not significantly different than early-maternal dens (Table 2; Fig. 2). We did not find support for

any of our other hypotheses about the biotic and environmental factors influencing cavity site selection (Table 2). Litter survival at early-maternal dens was not significantly different from litter survival at natal dens (mean intercept on the logit scale = 2.24,

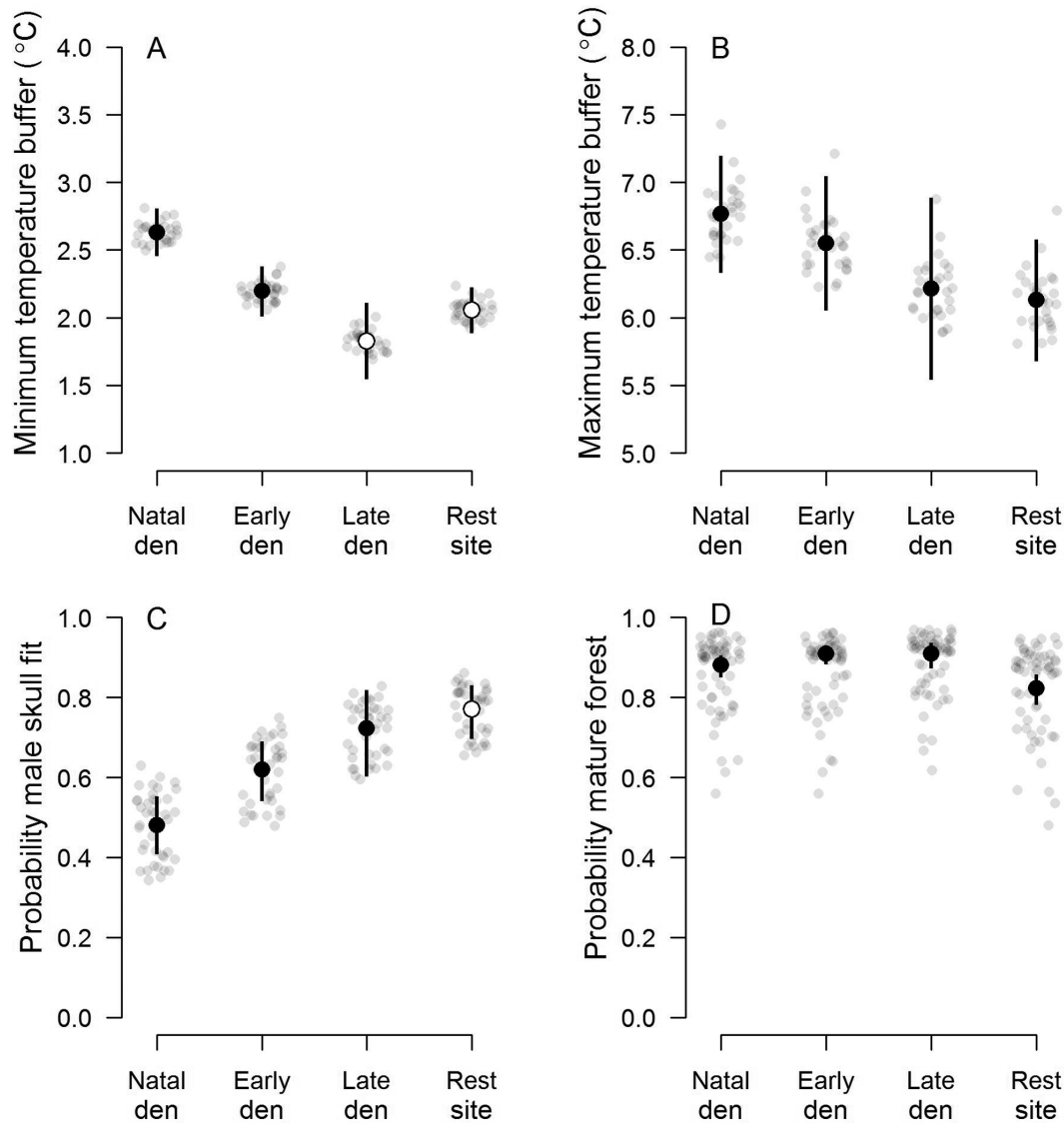


Fig. 2.—Relationships among characteristics of reproductive dens and cavity rest sites selected by fishers (*Pekania pennanti*). A) Minimum temperature buffer, B) maximum temperature buffer, C) the probability of a male skull fitting through the cavity opening, and D) the probability the den or rest site was located in mature older forest on the Hoopa Indian Valley Reservation in northern California between 2005 and 2016. Large circles and vertical lines indicate the mean $\pm$ SD of the posterior parameter effect. Closed black circles indicate no significant differences among groups, whereas open circles indicate significant differences from the natal den (95% CI for the effect did not overlap 0). Each gray circle represents the modeled random effect for each female fisher.

$SD = 0.22$, $CI = -0.2, 4.86$; early-maternal den effect on the logit scale = 0.51 , $SD = 0.39$, $CI = -0.24, 1.28$). Litter survival, however, was significantly greater at late-maternal dens than at natal dens (late-maternal den effect on the logit scale = 1.51 , $SD = 0.59$, $CI = 0.42, 2.72$; Fig. 3). The age of adult female fishers did not affect the probability of litter survival (age effect on the logit scale = 0.21 , $SD = 0.21$, $CI = -0.21, 0.63$). All models provided sufficient fit ($0.1 < \text{Bayesian } P\text{-value} < 0.9$).

DISCUSSION

The developmental period immediately postpartum is a particularly vulnerable time for mammalian offspring and energetically taxing for mammalian females (Ofstedal and Gittleman

1989; Millar 2007; Miller et al. 2014). In fishers, certain aspects of their reproductive biology and the selection of particular reproductive den characteristics may influence the likelihood of raising a litter to weaning and the vulnerability of adult females to mortality (Sweitzer et al. 2016). Powell and Leonard (1983) and Powell (1993) reported the energy expenditure of a lactating female fisher is approximately three times greater than a female's estimated expenditure before parturition. The timing of breeding and parturition have been decoupled in fishers through delayed implantation (Hall 1942; Enders and Pearson 1943), with mating occurring within 10 days after females give birth (Powell 1993). Thus, breeding likely imposes additional energetic costs and stresses for female fishers during early kit development as females must give birth, care for newborns,

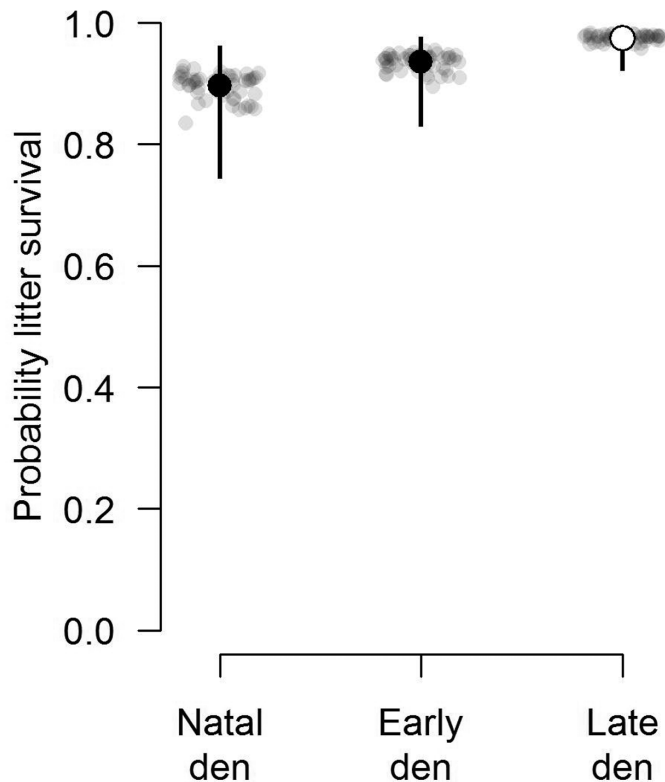


Fig. 3.—Differences in the posterior probability of fisher (*Pekania pennanti*) litter survival among reproductive den cavities on the Hoopa Indian Valley Reservation in northern California between 2005 and 2016. Survival was significantly higher at late-maternal dens than at natal dens. There was no difference between survival at natal dens and early-maternal dens (95% *CI* for the effect did not overlap 0). We present the mean and *SD* of the posterior distribution. Each gray circle represents the modeled posterior random effect for each female fisher.

interact with potential mates, and obtain prey to maintain their own energetic needs all within a condensed period of time (Powell 1993).

A wide range of genetic, phenotypic, and environmental factors likely influence reproductive success in wild fishers (Matthews et al. 2013; Sweitzer et al. 2016; Green et al. 2017). We found both sex and age had significant effects on weight of kits between 17 and 67 days postpartum. Our findings on kit development in the wild differ from the only previously reported results from captivity. Frost and Krohn (2004) found no difference in body weight between males and females 30 days postpartum but that males became larger than females by 60 days postpartum. Similarly, Powell (1993) summarized data from Coulter (1966), Kline and Don Carlos (Minnesota Zoological Society, unpubl. data), and LaBarge et al. (1990) and found that noticeable differences in weight between male and female kits born in captivity were not apparent until around 90 days postpartum. Evidence for heavier male kits and similarities in length between male and female kits in Hoopa suggests female fishers may be preferentially investing in male kits in the current study. Trivers and Willard (1973) proposed that maternal condition in dimorphic, polygynous mammals could influence the sex ratio of offspring, and females in better than average condition should

favor male offspring to yield the highest marginal fitness returns. Empirical evidence to support the theoretical model, however, remains controversial (Williams 1979; Clutton-Brock and Iason 1986; Hewison and Gaillard 1999; Sheldon and West 2004).

Patterns of habitat selection by fishers are strongest and most consistent at fine spatial scales (Lofroth et al. 2010; Raley et al. 2012; U.S. Fish and Wildlife Service 2016b). Fishers tend to select home ranges and resting sites in areas of complex forest structure that provide sufficient prey, escape cover, and suitable microstructures for reproduction and resting (Raley et al. 2012; Aubry et al. 2013). Limited information, however, is available on patterns of den selection, the possible consequences for neonates, and subsequent forest management recommendations. Fishers in other parts of the western United States and British Columbia selected dens in complex forests with large trees and snags, dense canopy cover, and decay on steep slopes (Weir et al. 2012; Zhao et al. 2012; Green 2017). These characteristics may influence den selection due in part to the availability of cavities and other structures used for resting and their importance to potential prey (Zielinski et al. 2004a; Raley et al. 2012; Green 2017).

We, however, did not find evidence that reproductive dens in Hoopa were located more frequently in stands of mature forest, in forest patches with more opportunities to escape predators in the form of vertical forest structure, or located closer to forest stands with large prey abundances. We suspect these results may be a function of forest management history in Hoopa, whereby historic and contemporary logging activities have retained structural components selected by fishers for reproductive dens and cavity rest sites (J. Mark Higley, Hoopa Tribal Forestry, pers. comm., August 2018). These forest management practices coupled with the inherently high availability of prey in Douglas-fir–tanoak forests (Sakai and Noon 1993) might limit the influence of prey availability during the reproductive season. This explanation is supported by the relatively small sizes of home ranges of female fishers in our study compared to those in other parts of the geographic range of fishers (Rennie 2015; Furnas et al. 2017). It is also possible that female fishers forage away from the den to reduce predation risk, meet increased energetic demands during kit rearing, or to maintain their territory.

Selection of reproductive dens in Hoopa appeared strongest at the spatial scale of the cavity. Female fishers in our study selected natal dens with smaller cavity openings than those of cavity rest sites, limiting or preventing access of male fishers and larger-bodied predators. Similarly, Weir et al. (2012) reported the narrowest dimension of 31 reproductive den cavity openings found in northeastern British Columbia were only slightly larger than female fisher skull measurements. Additionally, the cavity openings of fisher reproductive dens used early in the reproductive season were reported to be smaller than those used later in the reproductive season in New England (before versus after 1 May—Powell et al. 1997) and in the Sierra Nevada (natal versus maternal—Green et al. 2017), but were not significantly different in Maine (natal versus maternal—Paragi et al. 1996). Powell et al. (1997) concluded that females selected cavities with openings that excluded larger animals, particularly predators, but did not address the

influence of male fishers. Female fishers may select cavities with small openings to provide opportunity for mate choice outside the reproductive den because mating occurs shortly after parturition (Clutton-Brock and McAuliffe 2009), conserve energy by dictating the timing of mating (Powell and Leonard 1983), avoid harassment or infanticide of kits by male fishers (Dubruiel et al. 2013), and reduce risk of predation (Gabriel et al. 2015; Sweitzer et al. 2016).

We also found that female fishers selected natal and early-maternal dens that offered significantly more temperature insulation than late-maternal dens and rest sites. Similarly, Green (2017) reported natal dens offered more insulation than maternal dens in the southern Sierra Nevada of California. In the temperate climates and mid-elevations occupied by fishers, the period of parturition and early development in late March and early April frequently experience precipitation and low temperatures. The insulation properties we observed in natal and early-maternal dens indicate selection of cavities by female fishers to mitigate cold temperatures. Large live trees with limited decay buffer minimum temperatures better than smaller live trees and snags with more decay (Coombs et al. 2010; Cockle et al. 2015). We did not find evidence that reproductive den cavities and cavity rest sites differed significantly in buffering against high ambient temperatures observed later in the reproductive season.

Understanding the factors influencing survival of females and kits is an important area for future research given the current conservation concerns for fishers in the western United States (Raley et al. 2012; U.S. Fish and Wildlife Service 2016b). Our result indicating litter survival was greater at late-maternal dens than at natal and early-maternal dens further exemplifies the vulnerability of female fishers and their kits during the early developmental period from birth to 40 days old. Susceptibility of kits to a wide range of risk factors (e.g., exposure, malnutrition) and adult females to predation likely underlie litter survival. Extremely little is known about the sources of kit mortality in wild fishers. Limited information indicates that female fishers experience increased mortality in the spring and mid-summer, likely linked to the high energetic costs of reproduction (Sweitzer and Furnas 2016), the transition to a central-point foraging strategy, and the movement of kits between reproductive dens during kit rearing (Powell 1993).

Rest sites are the most studied element of fisher ecology in the Pacific states (Aubry et al. 2013). Our results illustrate characteristics differentiating cavity rest sites and reproductive dens, limiting our ability to extrapolate from factors thought to influence selection of rest sites to factors determining selection of reproductive dens. Further, although our knowledge of fisher rest-site characteristics is comprehensive, limited research exists examining how these rest sites affect the behavior, energetics, foraging success, or survival of fishers. Although suitable microsites used for resting have been found to be uncommon (e.g., Aubry et al. 2018), it remains undetermined whether the availability of rest sites may negatively affect fisher populations.

Forest management in the temperate, low- to mid-elevation forests occupied by fishers has the potential to reduce the abundance of trees and snags suitable for use as reproductive

dens (Proulx et al. 2004; Lofroth et al. 2010; Weir et al. 2012; U.S. Fish and Wildlife Service 2016b; Green 2017). Short harvest rotations, removal of tree species of limited commercial value, unnatural stocking to promote wood-fiber development, forest health policies intended to reduce the spread of tree diseases, wildfire suppression, and removal of hazard trees have likely negatively affected the distribution and abundance of trees with cavities (Lofroth et al. 2010; Weir et al. 2012; U.S. Fish and Wildlife Service 2016b). Fishers in Hoopa selected cavities with particular characteristics in primarily large, decayed tanoak trees for reproductive dens. These trees likely developed under very specific circumstances involving tree growth, damage agents (e.g., wind, low-intensity surface fires), fungal infection, and site conditions (Weir et al. 2012). The abundance and susceptibility of tanoak and Douglas-fir to damage, decay, and cavity development likely explain levels of use of these species by fishers for reproductive dens and cavity rest sites (Küchler 1977; Tappeiner et al. 1990). The conservation and recruitment of these structures will require the maintenance of natural processes that promote cavity genesis and development.

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SUPPLEMENTARY DATA

Supplementary Data SD1.—Proportions of live trees and snags used by female fishers (*Pekania pennanti*) as natal dens (a), early-maternal dens (b), late-maternal dens (c), and rest sites (d) on the Hoopa Valley Indian Reservation in northern California between 2005 and 2016. Tree species codes include AL (red alder, *Alnus rubra*), BO (California black oak, *Q. kelloggii*), CQ (giant chinquapin, *Chrysolepis chrysophylla*), DF (Douglas-fir, *Pseudotsuga menziesii*), HWD (unknown hardwood species), IC (incense cedar, *Calocedrus decurrens*), LO (California live oak, *Quercus agrifolia*), MD (madrone, *Arbutus menziesii*), MP (big leaf maple, *Acer acrophyllum*), PO (Port Orford cedar, *Chamaecyparis lawsoniana*), SP (sugar pine, *Pinus lambertiana*), TO (tanoak, *Notholithocarpus densiflorus*), WO (Oregon white oak, *Quercus garryana*), and UNK (unknown species).

Supplementary Data SD2.—Mean (points) and standard deviation (lines) of diameter at breast height (cm) of conifer (black) and hardwood (gray) trees and snags used as reproductive dens and cavity rest sites by female fishers (*Pekania pennanti*) on the Hoopa Valley Indian Reservation in northern California between 2005 and 2016.

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