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RESEARCH ARTICLE

Downed wood removal effects on survival and site fidelity of woodrats in a California oak woodland

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Abstract

Owing to the increasing intensity and frequency of wildfires in the western United States, the removal of woody debris (downed dead wood and snags) from fire-prone landscapes is being evaluated for wildfire mitigation. Consequently, the study of the ecological value of coarse woody debris to sustain dependent species has become of foremost importance. From 2004–2009, we used a before-after control-impact (BACI) study design to assess the effects of downed wood removal on a population of big-eared woodrats (*Neotoma macrotis*) in an oak woodland (*Quercus* spp.) in coastal-central California, USA. Using Pollock's robust design mark-recapture analyses (with 12 primary capture occasions represented by trapping each spring and fall, and secondary occasions composed of 3 trap nights), we estimated survival and emigration rates. Further, applying mixed-effects models, we evaluated the effects of 7 habitat attributes on woodrat abundance and reproduction. Following the experimental removal of downed wood from the 11 randomly selected treatment plots, woodrat survival was higher ($P = 0.013$), and emigration was lower ($P = 0.007$) among 11 control plots on which downed wood was retained. Woodrat abundance within plots was best predicted by stem density, demonstrating positive demographic associations with habitat complexity. Plot-level reproductive success (i.e., the presence of juveniles within a plot

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during spring) was more likely with increasing snag density. These findings indicate that snags and downed dead wood are key components of high-quality habitat for big-eared woodrats. Management of woody debris to mitigate wildfire risk should consider the ecological value of this habitat attribute for big-eared woodrats and other dependent species.

KEYWORDS

big-eared woodrat, coarse woody debris, downed wood, *Neotoma macrotis*, recruitment, robust design, snags

Coarse woody debris (i.e., downed wood and snags) is a valuable resource for a diverse array of wildlife and is particularly important for small mammals. Satisfying a variety of ecological needs, downed wood and snags provide nesting sites (Loeb 1999, Knowles and Burger 2008), daytime refugia for nocturnal species (Frank and Layne 1992, Hinkelman and Loeb 2007), travel lanes (Zollner and Crane 2003, Waldien et al. 2006), and foraging substrate for mycophagist and insectivorous small mammals (Tallmon and Mills 1994, Lee 2012).

In forest types across the United States, the demographic effects of coarse woody debris on small mammal populations vary widely. For example, in western hemlock (*Tsuga heterophylla*) forests in Washington, the fecundity and abundance of Trowbridge's shrews (*Sorex trowbridgii*) were higher on study sites with more snags and downed wood, whereas on those sites with less woody debris, vagrant shrews (*Sorex vagrans*) were more common (Lee 1995). Furthermore, Manning and Edge (2004) found that in Douglas-fir (*Pseudotsuga menziesii*) forests in Oregon, deer mouse (*Peromyscus maniculatus*) survival rates were highest among study plots with intermediate levels of downed wood; however, for creeping voles (*Microtus oregoni*), survival was better where downed wood was lacking. A final illustration comes from a mixed pine-hardwood forest in South Carolina where several tornadoes in 1989 generated considerable large woody debris. In the aftermath, cotton mice (*Peromyscus gossypinus*) abundance was higher and adult female survival and reproductive success increased where coarse wood was not removed (Loeb 1999). However, research carried out in the same forest during the 11 years between 1996–2006 concluded that the population dynamics of cotton mice were not appreciably affected by the experimental removal or addition of snags and downed wood (Larsen-Gray et al. 2021). The above examples demonstrate that the complex relationships between coarse woody debris and small mammal demographics vary by species, forest type, and amount of woody debris.

Historically, wildfire or fire intentionally set for land management purposes in California oak woodlands (*Quercus* spp.) was seldom of sufficient intensity to remove most large woody debris. However, in recent decades the state's oak woodlands have been heavily influenced by factors that affect both the production and removal of downed wood and snags. These include intense and persistent drought (Mann and Gleick 2015, Das et al. 2019), disease-related mortality caused by *Phytophthora ramorum* (i.e., sudden oak death; Kovacs et al. 2011, He et al. 2021), and invasive insect pests such as the goldspotted oak borer (*Agrilus auroguttatus*) and polyphagous shot hole borer (*Euwallacea* spp.; Coleman et al. 2008, 2012, 2019). Even so, the most consequential influence on downed wood and snags has been wildfires that, over the past century, have increased in frequency, size, and intensity (Wells et al. 2004).

The heightened risk of increasingly severe wildfire has prompted serious discussion about the costs and benefits of the removal of coarse woody debris as a management strategy to reduce wildfire risk (Converse et al. 2006, Hutto 2006). The techniques being discussed are manual removal and prescribed burning, each having impacts on wildlife that vary with the practice used, site-specific environmental variables, and the measure of woody debris removed (Stephens et al. 2012). Previous research indicates that, although prescribed burning may reduce some attributes of habitat quality, this management option can effectively reduce wildfire risk while leaving snags and downed wood intact or only partially consumed (Vreeland and Tietje 1998, Stephens et al. 2012).

Accordingly, a greater awareness of the effects of fuel management practices on dependent wildlife is warranted to safeguard the biological integrity of the treated woodlands (Greenberg et al. 2018*a*, *b*; Grodsky et al. 2018).

Coastal California oak woodlands provide essential habitat for 2 ecologically similar species of woodrats: the dusky-footed woodrat (*Neotoma fuscipes*) and the big-eared woodrat (*N. macrotis*; Matocq 2002). Both species inhabit oak woodland with a complex understory where they serve as primary prey for a diversity of reptilian, mammalian, and avian predators (Brylski 1999*a*, *b*). They construct large, conspicuous, dome-shaped houses from fine woody debris (i.e., sticks, twigs, and bark; Linsdale and Tevis 1951, Whitford and Steinberger 2010). These stick houses moderate temperatures (Brown 1968) and are used for rearing young and food storage (Carraway and Verts 1991). The importance of fine woody debris in the construction of woodrat houses is well known; however, the incorporation of coarse wood in these houses and its influence on woodrat demographic patterns have not been examined.

Using a before-after control-impact (BACI) study design, we investigated the effects of downed wood (logs ≥7.6 cm in diameter) removal on big-eared woodrat abundance, survival, site fidelity, and reproduction. Further, we assessed the influence of several other habitat attributes and snags on these demographic parameters. We predicted that downed wood removal would negatively influence woodrat abundance, site fidelity, and rates of reproduction and survival. Taken together, we expected that our study would demonstrate that downed wood and snags are significant components of high-quality habitat for big-eared woodrats by contributing to the conditions appropriate for individual and population persistence (Hall et al. 1997).

STUDY AREA

We conducted our study in coastal-central California, in a remote area of the National Guard Post, Camp Roberts, California, USA, from 2004 to 2009 (Figure 1). Our 22 1.1-ha study plots were distributed across an 8,000-ha oak woodland matrix of grassland, chaparral, and woodland that lies on the range boundary of the big-eared woodrat and dusky-footed woodrat. The elevation on the study area ranged from 268 m to 480 m. Topography varied from gently rolling to slopes ≤30°. The climate is Mediterranean, characterized by 2 distinct seasonal periods: cool, wet winters (Nov–Apr) and warm, dry summers (May–Oct). During the 6-year study, annual precipitation averaged 40.2 cm but was highly variable (6-yr range = 19.7–61.5 cm; National Oceanic and Atmospheric Administration 2016). Nearly all (97%) precipitation fell between November and April. Average temperatures ranged from 1.7°C in the coolest winter month (Jan) to 14°C during the warmest month (Jul). Public access to the areas of Camp Roberts that included our study plots was limited to hunting within the statewide seasons. No military activity or public use had altered coarse woody debris or any vegetative structural component on the study area, and the most recent wildfire was 51 years prior to the initiation of our study.

The more xeric woodlands in the study area consisted of stands of blue oak (*Q. douglasii*) trees with an understory of scattered buckbrush (*Ceonothus cuneatus*), hollyleaf redberry (*Rhamnus ilicifolia*), bigberry manzanita (*Arctostaphylos glauca*), and chamise (*Adenostoma fasciculatum*). The ground layer of these woodlands was dominated by Mediterranean annual grasses, wild oats (*Avena* spp.), and brome (*Bromus* spp.), with scattered native bunchgrasses (nodding needlegrass [*Nassella* spp.] and fescue [*Festuca* spp.]). In the more mesic areas, blue oak and coast live oak (*Q. agrifolia*) trees co-occurred, with a diverse shrub understory consisting of toyon (*Heteromeles arbutifolia*), California coffeeberry (*Frangula californica*), hollyleaf redberry, buckbrush, and bigberry manzanita. Ground cover was characterized by patches of grass intermixed with an assemblage of native and exotic forbs, including wild peony (*Paeonia californica*), hummingbird sage (*Salvia spathacea*), and miner's lettuce (*Claytonia perfoliata*). Poison oak (*Toxicodendron diversilobum*) occurred throughout the study area, varying in density from scattered stems to homogeneous patches covering <0.25 ha. Within these vegetation communities, suspected predators of big-eared woodrats included great horned owl (*Bubo virginianus*), California spotted owl (*Strix occidentalis occidentalis*), northern Pacific rattlesnake (*Crotalus oreganus oreganus*), Pacific gopher snake (*Pituophis catenifer catenifer*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), and gray fox (*Urocyon cinereoargenteus*; Brylski 1999*b*).

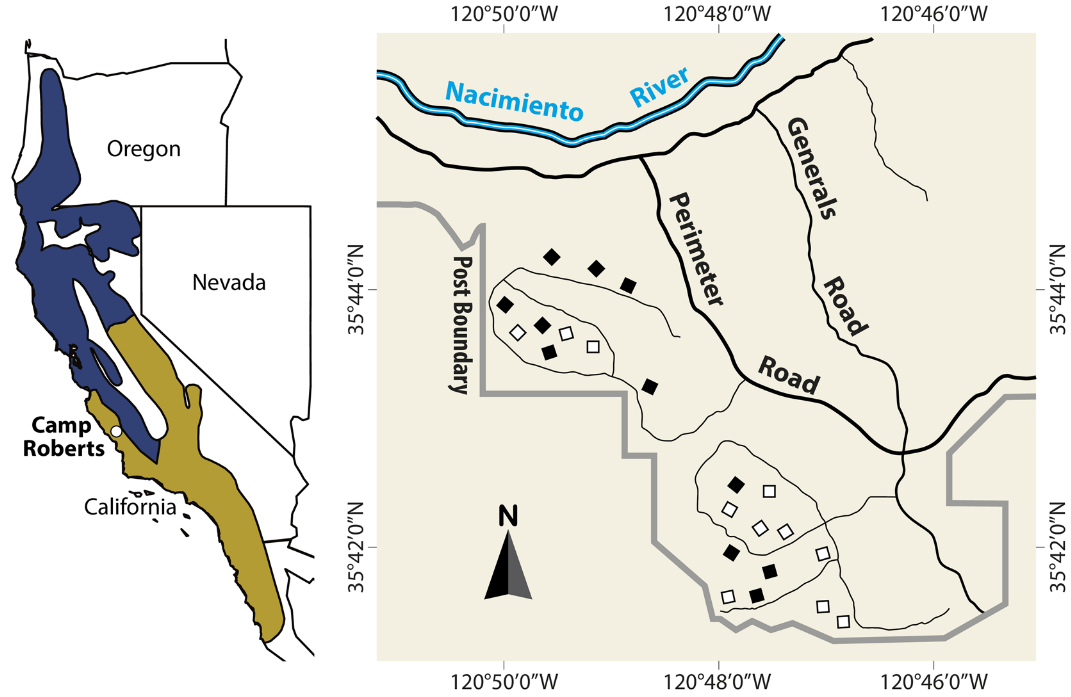

FIGURE 1 Study area map showing the location of Camp Roberts, California, USA, (white circle in the overview map). The range of the big-eared woodrat is shown in gold and the range of dusky-footed woodrat in blue. We conducted live trapping from 2004 to 2009 in May and October on 22 1.1-ha study plots (treatment plots are represented as open squares and control plots as solid black squares) to evaluate the demographic response of big-eared woodrats to the experimental removal of downed dead wood (≥7.6 cm diameter). The study plot map is not drawn to scale. Overview map is reprinted from Hunter et al. (2017:3899), with permission from Elsevier.

METHODS

Field sampling

From 2004–2009, we conducted 3 consecutive nights of trapping in each of the 22 1.1-ha plots (traps placed in 8 × 8 grids at 15-m intervals) in spring (May) and again in fall (Oct), with plots separated by 50 m to 2 km. Previous analyses of mark-recapture data collected for big-eared woodrats demonstrated that 3 consecutive nights of trapping at ≥5-month intervals, as conducted here, did not negatively affect the apparent survival of captured individuals (Hardy et al. 2013). During the 3 trap nights, we placed a live trap (model LNG12; 7.6 × 8.9 × 30 cm; H.B. Sherman Traps, Tallahassee, FL, USA) at each of the 64 grid intersections in the 1.1-ha plot, checking traps daily. To protect trapped animals from cool temperatures at night and warm early morning sunshine, we placed traps in the shade within 2 m of grid intersections and covered the top with litter from the immediate vicinity. We baited traps with a mixture of rolled oats, corn, and barley. Upon initial capture, we placed a numbered tag (Monel 1005-1L1, National Band and Tag Company, Newport, KY, USA) in the right ear of woodrats and recorded tag number, trap location, sex, and age (juvenile if >25% gray pelage, otherwise adult, as juveniles transition to adult pelage within 4 months of age). Following handling, we released woodrats at the site of capture.

Hereafter, we use the term downed wood to refer to dead wood in contact with the ground, and the term coarse woody debris to refer collectively to downed wood and snags (standing dead trees). Because we suspected that snags and downed wood fill distinct ecological needs for woodrats, we used sampling protocols that allowed us to independently quantify the availability of snags and downed wood.

During January 2007, we sampled downed wood at alternate grid intersections on each trapping grid ($n = 32$ sampling points/plot placed at alternate non-overlapping grid intersections) using methods adapted from the United States Forest Service Pacific Northwest Forest Inventory and Analysis protocol (Waddell 2002:144–145). Specifically, centered on each sampling point, we established 4 10-m transects oriented in the 4 cardinal directions (1,280 m of transect/plot). We tallied all pieces of downed wood that crossed ≥1 transect and were ≥7.6 cm in diameter at the point of intersection, ≥1 m long, and in contact with the ground for ≥1 m of their length (Bate et al. 2002). We based these criteria on the assumption that downed wood with the preceding measurements would provide cover for woodrats. For each intersected piece, we recorded the length that was ≥7.6 cm in diameter and the diameter at the small (≥7.6 cm) and large ends. We did not tally limbs that contacted the ground if still attached to a standing tree. If a forked piece of downed wood was intersected, we measured only the length of the intersected branch, whereas if multiple branches of a forked piece were intersected, we tallied each branch separately. Finally, we tallied a piece twice if it intersected the same transect twice (curved log) or if it intersected 2 transect lines. From these measurements, we used Smalian's equation (Husch et al. 1972) to calculate the volume (m^3) of downed wood and determined the density of downed wood pieces (pieces/1.1-ha study plot) within each of our 22 study plots.

To ensure that control and treatment groups were balanced for the experimental removal of downed wood, we ranked the 22 plots by downed wood volume and paired the plot with the most downed wood with the second most downed wood, and so forth, to establish 11 pairs of plots. We then randomly assigned 1 plot from each pairing to the treatment group and the remaining one to the control group (Table S1, available in Supporting Information) in accord with a BACI study design.

From January to March 2007, an inmate firefighter crew from the California Department of Forestry and Fire Protection (CAL FIRE) removed all downed wood from the 11 treatment plots. Crew members removed downed wood by hand, using chain saws to cut the larger pieces when necessary. They piled the downed wood outside of the plots where they burned it. Except for chain saws, crews did not use any equipment. The only disturbance to soil or woody vegetation was a consequence of dragging larger pieces of downed wood out of treatment plots. Throughout the downed wood removal process, crews did not disturb woodrat houses. The same CAL FIRE crew was present for each day of removal, providing consistency across treatment plots.

In summer 2007, we used the point-center-quarter method (Cottam and Curtis 1956) to sample habitat attributes at 2 randomly selected non-adjacent grid intersections on alternate lines of each of the 22 study plots ($n = 8$ sample points/plot). Within a 10-m radius of each of the randomly selected points, we recorded the following measurements for each of the NE, SE, SW, NW quadrants: the distance to the nearest live tree and the associated diameter at breast height (dbh; dbh ≥10 cm), the distance to the nearest snag (we included bigberry manzanita when meeting the size criteria to be classified as a tree or snag, dbh ≥10 cm), and the distance to the nearest woody stem (excluding poison oak) ≥1.35 m in height and of any dbh. Species included in this final metric were toyon, California coffeeberry, hollyleaf redberry, buckbrush, bigberry manzanita, chamise, oak snags, live trees, and saplings. We used the density formula given in Cottam and Curtis (1956) to calculate live tree, snag, and stem densities for each of the 1.1 ha study plots. To account for quadrants without a live tree, snag, shrub, or sapling, we used the correction factor described by Warde and Petranka (1981).

Statistical analyses

We analyzed woodrat capture-recapture data using Pollock's robust design model (Kendall et al. 1995, 1997) implemented in Program MARK 6.2 (White and Burnham 1999). We treated spring (May) and fall (Oct) trapping (conducted 2004–2009) as primary capture occasions and the 3 trap-nights within each primary occasion as secondary capture occasions. The robust design model integrates the following parameters: 2 parameters relating to capture probability (initial capture probability within primary occasion *i* [p_i] and recapture probability within primary occasion *i* [c_i]), 1 parameter representing survival from primary occasion *i* to primary occasion *i* + 1 (S_i), and 2 parameters related to temporary emigration (the probability of being off the study area and unavailable for capture during primary occasion *i*, given that the animal was not present on the study area during occasion *i* - 1 [γ'_i] and the probability of being off the study area and unavailable for capture during primary occasion *i*, given that the animal was present on the study area during occasion *i* - 1 [γ''_i]; Kendall 2023).

Prior to fitting robust design models, it is necessary to evaluate the goodness of fit of the general model. Given that a goodness-of-fit test has not been developed for the robust design model, we evaluated the corresponding closed-population model in Program MARK following the bootstrap procedure described by Cooch and White (2022). Reflective of the structure of the general robust design model (described below), we allowed capture probability (*p*) and apparent survival (φ) to vary with age, sex, and time (i.e., primary occasions within the robust design as described above). Specifically, we conducted 1,000 bootstrap iterations of the model $\varphi_{(\text{group}\times\text{time})}$ $p_{(\text{group}\times\text{time})}$ in which groups represented juvenile females, juvenile males, adult females, and adult males. To evaluate goodness of fit, we then evaluated the observed model deviance relative to the distribution of the deviances from the 1,000 simulated iterations. In the same manner, we corrected for overdispersion ($\hat{c}$) by evaluating $\hat{c}$ from the observed model relative to the distribution of $\hat{c}$ from the 1,000 simulated iterations. For this we also followed the recommendations of Cooch and White (2022) to calculate $\hat{c}$ using the following 2 approaches: the observed model deviance divided by the mean deviance derived from 1,000 simulated iterations and the observed value of $\hat{c}$ divided by the mean $\hat{c}$ from the 1,000 simulated iterations. We then retained the greater (i.e., more conservative) of the $\hat{c}$ values to use as an overdispersion correction factor when evaluating competing robust design models.

After assessing goodness of fit and overdispersion, we evaluated alternative configurations of robust design models. Specifically, we evaluated these models with 2 distinct objectives: describe woodrat detection rates and demographic processes that contributed to the observed encounter histories (process model) and build upon the process model to test specific hypotheses regarding the BACI design and the influence of habitat attributes on woodrat demographic parameters. In the formulation of the process model, we evaluated competing model structures that described capture probability (*p*) as a function of age (juvenile vs. adult), sex, and capture occasion (i.e., a categorical variable representing the primary capture occasions). Because we had insufficient data for model convergence to treat all primary capture occasions as independent categorical variables, we evaluated survival (*S*) as a function of age, sex, and occasion, and we evaluated emigration (γ'') as a function of age, sex, and season (spring [May] vs. fall [Oct]). To avoid fitting overly complex models, we assumed no behavioral effect on capture probability (e.g., trap happiness or trap shyness) within each primary occasion (i.e., recapture probability [*c*] = capture probability [*p*]). Additionally, because of challenges with model convergence, we used an intercept-only model to represent the component of temporary emigration described within the robust design as γ' (i.e., the probability of remaining outside of study plots and unavailable for capture during both the current and previous primary capture occasions). The biological interpretation of the necessary simplification of using an intercept-only model was that we modeled the probability of remaining outside of study plots as a random process.

Formulation of the process model was foundational for evaluating the response of woodrat demographic rates to experimental downed wood removal and to evaluate the other habitat attributes that we measured. Accordingly, we used quasi-Akaike's Information Criterion corrected for small sample size (QAIC_c) to evaluate competing robust design models that included all combinations of the covariates listed above ($n = 512$ models that included all combinations of age, sex, and time among robust design model components *p*, *S*, and γ''; Doherty et al. 2012). After identifying the best-supported robust design process model as determined by the lowest QAIC_c value (Burnham and Anderson 2002), we built upon the process model in Program MARK by adding additional categorical variables that reflected the BACI design, differentiating control versus treatment plots and the time periods before and after downed wood removal. With these factors added to the process model, using likelihood ratio tests to evaluate statistical significance, we tested for differences in survival between control and treatment plots before and after downed wood removal. Then, applying the same model configuration of the process model with BACI categorical variables, we evaluated differences in emigration between control and treatment plots before and after the downed wood was removed.

To investigate the effects of habitat attributes on woodrat survival and emigration rates, we expanded the process model to include linear and quadratic measures of these 7 plot-level habitat components: 1) density of live trees (trees/ha), 2) dbh of live trees, 3) density of stems (trees + shrubs/ha), 4) dbh of snags, 5) density of snags (standing dead trees/ha), 6) density of downed wood (pieces/ha), and 7) volume of downed wood (m^3/ha). To facilitate interpretation among disparate habitat attributes, we centered and scaled all habitat attributes to a mean of 0 and a standard deviation of 1. Given the potential for correlation among habitat attributes, we restricted our suite of candidate models to the process model with the addition of an individual habitat attribute in both a linear and a linear + quadratic form.

During the post-treatment period, we assigned all treatment plots a value of 0 for density and volume of downed wood. We recognize that an unknown amount of downed wood might have accumulated on treatment plots from fallen snags or live trees during the 3 years following removals. However, we would expect similar rates of incidental downed wood deposition on control plots. Thus, we believe the differences in downed wood between control and treatment plots represented in our models remained relatively consistent over the course of the study.

Given the potential for the removal of downed wood to change the importance of other habitat attributes on woodrat demographic rates, we conducted a preliminary evaluation to determine whether the association between demographic rates and habitat attributes changed with treatment or remained consistent throughout the duration of the study (e.g., separate βs that reflect the effect of tree density on survival before treatment and the effect of tree density on survival after treatment vs. a single β that reflects the tree density effect on survival for all periods, and so forth for the remaining 6 habitat attributes and demographic rates described above). This evaluation demonstrated that the underlying relationship between woodrat demographic rates and habitat attributes did not change in response to the treatment. Accordingly, we present only the models in which we used a single parameter to describe the association between habitat attributes and woodrat demographic rates, while allowing for the value of downed wood to change among treatment plots following removal (i.e., following removal, downed wood density and volume were set to 0 for treatment plots).

In addition to our investigation of woodrat survival and emigration rates, we evaluated linear mixed-effects models to describe the influence of downed wood removal and habitat characteristics on woodrat abundance. For this, we first used capture probabilities from the robust design process model, along with encounter histories, to estimate woodrat abundance on each plot during each primary capture occasion. We then evaluated the effect of the downed wood removal within the context of the BACI design, characterizing the plot and primary occasion as random effects and the downed wood removal treatment as a fixed effect, and fit models with the lme4 package (Bates et al. 2015) in Program R (R Core Team 2022). We also evaluated the relationship of woodrat abundance with linear and quadratic combinations of the 7 plot-level habitat attributes (centered and scaled) listed above. Similarly, we structured models evaluating abundance versus habitat attributes with plot and the primary capture occasion treated as random effects and habitat attributes as fixed effects.

Finally, we evaluated the ratio of the number of juvenile woodrats per adult female captured within plots as an index of reproductive rate. We equated ≥1 juvenile within a plot as reproductive success. Because most of the reproduction for big-eared woodrats on our study area occurred in late winter and early spring (88% of juveniles encountered in this study were captured during May trapping), we restricted this analysis to data from the May primary capture occasions. Even restricting this analysis to the May primary capture occasions, we still failed to capture a juvenile within some study plots, suggestive of plot-level reproductive failure. Therefore, we used zero-inflated mixed-effects models using package glmmTMB (Brooks et al. 2017) in Program R (R Core Team 2022) to model factors influencing reproduction rate within plots. As in our assessments of woodrat abundance, we evaluated the effects of the density and volume of downed wood that we removed (control vs. treatment as a categorical fixed effect) on reproductive rates. Additionally, we evaluated plot-level reproduction rate relative to the 7 habitat attributes. We considered both linear and quadratic combinations of habitat attributes as fixed effects and included the plot and primary occasion as random effects in all models.

RESULTS

Our cumulative trapping effort, conducted from spring 2004 to fall 2009, represented 50,688 trap-nights (64 traps × 3 trap-nights/session × 22 plots × 6 spring and 6 fall primary capture occasions). We censored 23 encounters that resulted in trap-related mortalities (representing 0.3% of woodrat captures and 0.9% of individual woodrats encountered) and 39 encounters in which we did not determine age or sex. So that we could reliably assign animals to plots within each primary occasion, we also excluded 30 woodrat encounters from the data set (1.22% of individuals captured) in which woodrats moved among plots (Figure 1) within a given primary occasion. Consequently, we included 6,817 captures of 2,432 woodrats in our analyses ($\bar{x} \pm SD = 2.80 \pm 2.28$ captures/individual). Females comprised 49.1–69.4% (57.6 ± 6.6%) of captures across the 12 primary capture occasions and juveniles accounted for 2.2–11.5% (8.2 ± 3.3%) of captures during the 6 spring occasions.

Robust design model selection

The goodness-of-fit evaluation of the full model $\varphi_{(\text{group}\times\text{time})}$ $p_{(\text{group}\times\text{time})}$ within a closed-population framework demonstrated adequate fit ($P > 0.368$) to warrant evaluation of reduced forms of the model within a robust design framework. In calculating $\hat{c}$ as a variance inflation factor for evaluating competing robust design models, the method using the observed model deviance divided by mean deviance from simulated iterations yielded an estimate of 1.019, whereas the method using observed $\hat{c}$ divided by mean $\hat{c}$ from simulated iterations yielded an estimate of 1.010. Accordingly, we carried forward the more conservative $\hat{c}$ of 1.019 to evaluate competing robust design models with $QAIC_c$.

Evaluating competing robust design models that included all combinations of age, sex, and time ($n = 512$), the best model (lowest $QAIC_c$) included capture (p) and survival (S) as a function of age, sex, and primary occasion and emigration (γ'') as a function of sex (Table S2, available in Supporting Information). One other model was competitive ($\Delta QAIC_c = 1.437$), which included season as an additional covariate in the estimation of emigration. Given that the best model was a reduced version of the only other competitive model, we interpreted this as strong support for the best model. Accordingly, we treated the best model as the process model to serve as a foundation in testing specific hypotheses regarding the response of big-eared woodrats to downed wood removal and the influence of habitat attributes on demographic rates.

Based on parameter estimates derived from the process model, capture probabilities were higher for female than male woodrats ($\beta_{\text{sex}} = 0.261$, SE = 0.049, $p_{\text{female}} = 0.439$, 95% CI = 0.399–0.480 vs. $p_{\text{male}} = 0.372$, 95% CI = 0.356–0.389) and for adults than juveniles ($\beta_{\text{age}} = -0.844$, SE = 0.127, $p_{\text{juvenile}} = 0.264$, 95% CI = 0.212–0.324 vs. $p_{\text{adult}} = 0.418$, 95% CI = 0.407–0.430). Capture probabilities were variable among primary occasions with no clear pattern, as 95% confidence intervals demonstrated substantial overlap among individual occasions. Similarly, survival rates showed no discernible pattern over time, with most primary occasions not deviating significantly from the overall mean; however, survival was higher for females ($\beta_{\text{sex}} = 0.289$, SE = 0.057, annual survival $S_{\text{female}} = 0.465$, 95% CI = 0.394–0.532 vs. $S_{\text{male}} = 0.361$, 95% CI = 0.330–0.392), and higher for adults than juveniles ($\beta_{\text{age}} = -0.412$, SE = 0.146, annual survival $S_{\text{adult}} = 0.430$, 95% CI = 0.407–0.453 vs. $S_{\text{juvenile}} = 0.215$, 95% CI = 0.123–0.325). Emigration (γ'') was higher for males than females ($\beta_{\text{sex}} = -0.399$, SE = 0.175, $\gamma''_{\text{female}} = 0.221$, 95% CI = 0.134–0.341, vs. $\gamma''_{\text{male}} = 0.297$, 95% CI = 0.246–0.354).

Survival did not differ between control and treatment plots before downed wood was removed ($\beta_{\text{before-treatment}} = -0.0001$, SE = 0.079, $\chi^2_1 = 0.0$, $P \sim 1$). After downed wood removal, survival was higher among the 11 control plots compared to the 11 treatment plots ($\beta_{\text{after-treatment}} = -0.210$, SE = 0.084, $\chi^2_1 = 6.170$, $P = 0.013$). Specifically, estimated annual survival among the control plots was 47% ($S_{\text{after-control}} = 0.474$, 95% CI = 0.424–0.516) relative to 40% among treatment plots ($S_{\text{after-treatment}} = 0.400$, 95% CI = 0.297–0.501). Like survival, emigration (γ'') rates did not differ between control and treatment plots before downed wood was removed ($\beta_{\text{before-treatment}} = -0.127$, SE = 0.217, $\chi^2_1 = 0.346$, $P = 0.557$). After downed wood removal, emigration rates were lower among control plots as compared to treatment plots ($\beta_{\text{after-treatment}} = 0.635$, SE = 0.242, $\chi^2_1 = 7.214$, $P = 0.007$) with an estimated 17% emigration rate among control plots ($\gamma''_{\text{after-control}} = 0.165$, 95% CI = 0.113–0.233) relative to 28% among treatment plots ($\gamma''_{\text{after-treatment}} = 0.281$, 95% CI = 0.136–0.492).

In our evaluation of the associations between survival and habitat attributes, woodrat survival was best predicted by the volume of downed wood with survival rates increasing with increasing downed wood volume ($\beta_{\text{downed wood volume}} = 0.135$, SE = 0.032, $\chi^2_1 = 18.872$, $P < 0.001$; Table 1; Figure 2A). The model that included the linear and quadratic combination of downed wood volume was also competitive ($\Delta\text{QAIC}_c = 1.91$; Table 1). During the period prior to downed wood removal, predicted annual survival ranged from 0.322 (minimum downed wood volume = 0.31 m^3/ha) to 0.505 (maximum downed wood volume = 21.02 m^3/ha). Following downed wood removal,

TABLE 1 Model rankings based on quasi-Akaike's Information Criterion corrected for small sample size (QAIC_c) of big-eared woodrat survival (*S*) relative to habitat attributes among 1.1-ha study plots established on Camp Roberts, California, USA, from 2004–2009, with model weights (w_i), model likelihoods, number of parameters, and quasi-deviance scores also presented. Competing models illustrate plot-level measures of habitat attributes added to the best Pollock's robust design model, in which survival (*S*) varied as a function of age (juvenile vs. adult), sex, and occasion (a categorical variable describing the 12 primary capture occasions conducted in May and Oct of 2004–2009), probability of capture (*p*) varied as a function of age, sex, and occasion, and temporary emigration (γ'') varied as a function of sex (temporary emigration [γ'] was modeled as an intercept-only).

Model[a]	QAIC_c	Delta QAIC_c	w_i	Model likelihood	Number of parameters	Quasi-deviance
S(age + sex + occasion + downed wood vol)	24,302.32	0.00	0.60	1.00	31	24,692.60
S(age + sex + occasion + downed wood vol^2)	24,304.23	1.91	0.23	0.39	32	24,692.48
S(age + sex + occasion + snag density)	24,306.73	4.41	0.07	0.11	31	24,697.09
S(age + sex + occasion + snag density^2)	24,307.39	5.07	0.05	0.08	32	24,695.70
S(age + sex + occasion + downed wood density)	24,308.30	5.98	0.03	0.05	31	24,698.68
S(age + sex + occasion + downed wood density^2)	24,309.45	7.13	0.02	0.03	32	24,697.80
S(age + sex + occasion + stem density^2)	24,312.25	9.93	0.00	0.01	32	24,700.65
S(age + sex + occasion + tree density^2)	24,316.29	13.97	0.00	0.00	32	24,704.77
S(age + sex + occasion + tree dbh)	24,317.46	15.14	0.00	0.00	31	24,708.02
S(age + sex + occasion + snag dbh)	24,317.90	15.57	0.00	0.00	31	24,708.46
S(age + sex + occasion + tree dbh^2)	24,318.28	15.95	0.00	0.00	32	24,706.79
S(age + sex + occasion)	24,319.18	16.85	0.00	0.00	30	24,711.82
S(age + sex + occasion + snag dbh^2)	24,319.79	17.47	0.00	0.00	32	24,708.34
S(age + sex + occasion + tree density)	24,320.42	18.09	0.00	0.00	31	24,711.03
S(age + sex + occasion + stem density)	24,320.95	18.63	0.00	0.00	31	24,711.57

[a] Models with a quadratic term (i.e., ^{2}) included both the linear and quadratic representation of the given variable, with only the quadratic variable presented in the table for simplicity (e.g., *S*[age + sex + occasion + downed wood vol + downed wood vol^2]). Habitat attributes include downed wood volume (vol; m^3/ha), snag density (standing dead trees/ha), downed wood density (pieces/ha), stem density (live trees + shrubs/ha), tree density (live trees/ha), tree diameter at breast height (dbh), and snag dbh.

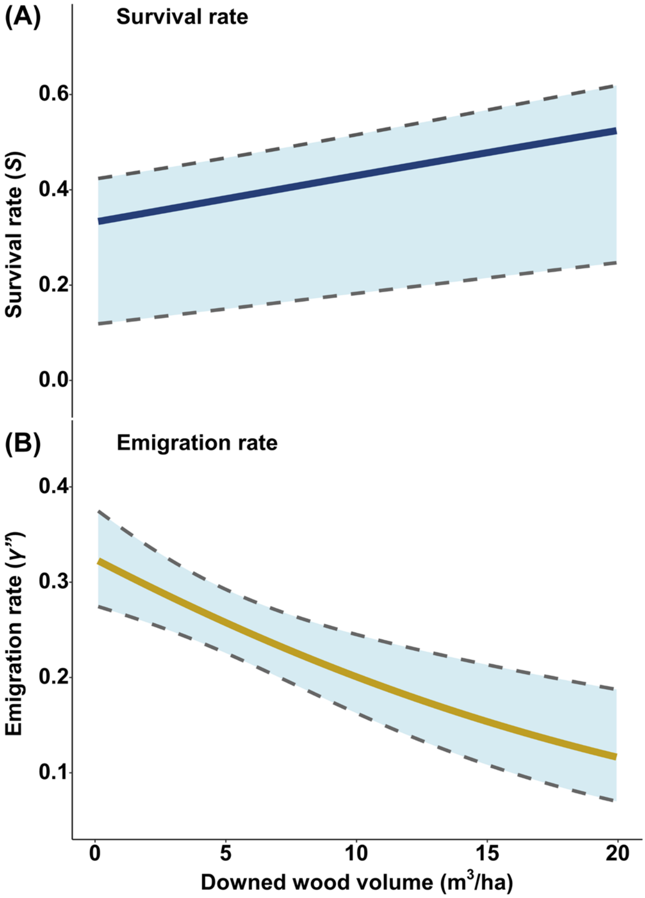

FIGURE 2 Relationships between volume of downed wood (m^3/ha) and the annual survival rate (A; blue line) and emigration rate (B; gold line) of big-eared woodrats captured on 22 1.1-ha study plots during 2004 to 2009 at Camp Roberts, California, USA. Dashed lines indicate 95% confidence intervals.

the predicted annual survival rate was 0.433 among treatment plots (with downed wood of 0 m^3/ha after experimental removal) versus predicted survival rates of 0.434 to 0.547 among control plots in which downed wood volume ranged from 0.31–15.16 m^3/ha.

Similarly, in our evaluation of habitat attributes and emigration, emigration rates were best predicted by the volume of downed wood ($\beta_{\text{downed wood volume}} = -0.306$, SE = 0.085, $\chi^2_1 = 14.124$, $P < 0.001$), although models that included the quadratic of downed wood volume and the density of downed wood were also competitive ($\Delta\text{QAIC}_c < 1.56$; Table 2). Emigration increased with decreasing downed wood volume (Figure 2B), with a predicted rate of 0.327 among treatment plots following the removal of downed wood (0 m^3/ha after experimental removal) versus predicted emigration rates of 0.322 to 0.159 among control plots (downed wood control range = 0.31–15.16 m^3/ha).

Woodrat abundance and reproduction rate

During the pre-treatment period, abundance estimates of woodrats ranged from 0–69 ($\bar{x} = 22.71 \pm 15.24$ [SD]) on control plots and 0–65 ($\bar{x} = 16.03 \pm 14.23$) on treatment plots; post-treatment, abundance ranged from 2–66 ($\bar{x} = 26.46 \pm 14.15$) on control plots and 0–42 ($\bar{x} = 19.52 \pm 12.00$) on treatment plots. Evaluation of the associations

TABLE 2 Model rankings based on quasi-Akaike's Information Criterion corrected for small sample size ($QAIC_c$) of big-eared woodrat temporary emigration (γ'') off of 1.1-ha study plots established on Camp Roberts, California, USA, from 2004–2009, with model weights (w_i), model likelihoods, number of parameters, and quasi-deviance scores also presented. Competing models illustrate plot-level measures of habitat attributes added to the best Pollock's robust design model, in which survival (*S*) varied as a function of age (juvenile vs. adult), sex, and occasion (a categorical variable describing the 12 capture occasions conducted in May and Oct of 2004–2009), probability of capture (*p*) varied as a function of age, sex, and occasion, and temporary emigration (γ'') varied as a function of sex (temporary emigration [γ'] was modeled as an intercept-only).

Model[a]	$QAIC_c$	Delta $QAIC_c$	w_i	Model likelihood	Number of parameters	Quasi-deviance
γ''(sex + downed wood vol)	24,307.07	0.00	0.32	1.00	31	24,244.78
γ''(sex + downed wood vol^2)	24,308.17	1.10	0.18	0.58	32	24,243.86
γ''(sex + downed wood density)	24,308.63	1.56	0.15	0.46	31	24,246.34
γ''(sex + downed wood density^2)	24,310.65	3.58	0.05	0.17	32	24,246.34
γ''(sex + snag density)	24,313.85	6.78	0.01	0.03	31	24,251.56
γ''(sex + tree dbh^2)	24,315.38	8.31	0.00	0.02	32	24,251.07
γ''(sex + snag density^2)	24,315.87	8.80	0.00	0.01	32	24,251.56
γ''(sex + tree dbh)	24,316.48	9.41	0.00	0.01	31	24,254.19
γ''(sex + stem density^2)	24,316.86	9.79	0.00	0.01	32	24,252.55
γ''(sex)	24,319.18	12.11	0.00	0.00	30	24,258.90
γ''(sex + tree density)	24,320.94	13.87	0.00	0.00	31	24,258.65
γ''(sex + stem density)	24,321.07	14.00	0.00	0.00	31	24,258.78
γ''(sex + snag dbh)	24,321.17	14.10	0.00	0.00	31	24,258.88
γ''(sex + tree density^2)	24,322.63	15.56	0.00	0.00	32	24,258.32
γ''(sex + snag dbh^2)	24,323.18	16.11	0.00	0.00	32	24,258.87

[a] Models with a quadratic term (i.e., ^{2}) included both the linear and quadratic representation of the given variable, with only the quadratic variable presented for simplicity (e.g., γ''[sex + downed wood vol + downed wood vol^2]). Habitat attributes include downed wood volume (vol; m^3/ha), downed wood density (pieces/ha), snag density (standing dead trees/ha), tree diameter at breast height (dbh), stem density (live trees + shrubs/ha), tree density (live trees/ha), and snag dbh.

between the BACI experimental design and woodrat abundance, without respect to continuous measures of habitat attributes, demonstrated no association with abundance ($P = 0.339$). Conversely, several of the habitat attributes evaluated were positively associated with woodrat abundance. The best model describing the association between habitat attributes and woodrat abundance was the quadratic stem density model ([trees + shrubs/ha] + [trees + shrubs/ha]^2; $\Delta AIC_c = 11.49$ for the next model; Figure 3; Table S3, available in Supporting Information). Abundance was predicted to peak at an intermediate stem density ($\beta_{\text{stem density}} = 10.662$, SE = 1.797; $\beta_{\text{stem density}^2} = -4.760$, SE = 1.075); abundance estimates ranged from 0 at the minimum stem density (97 stems/ha), increasing to 26 woodrats at the mean stem density (727 stems/ha), peaking at 32 woodrats at a stem density of 1,184 stems/ha, and decreasing to 23 woodrats at the maximum observed stem density (1,729 stems/ha). Other variables that were positively associated with abundance included tree density and snag density, whereas snag dbh and the density and volume of downed wood were not associated with abundance (Figure 3; Table S3).

Spring reproduction rates (i.e., juveniles/adult female) during the pre-treatment period ranged from 0–1.50 ($\bar{x} = 0.24 \pm 0.29$) on control plots and 0–1.67 ($\bar{x} = 0.28 \pm 0.38$) on treatment plots; post-treatment, reproduction rates ranged from 0–0.60 ($\bar{x} = 0.13 \pm 0.17$) on control plots and 0–0.75 ($\bar{x} = 0.15 \pm 0.19$) on treatment plots.

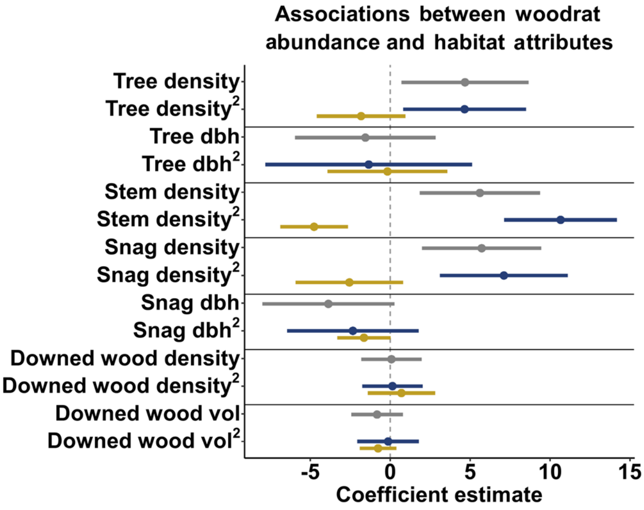

FIGURE 3 Linear mixed effects model beta coefficients illustrating the associations between big-eared woodrat abundance among 22 1.1-ha study plots on Camp Roberts, California, USA, and the following habitat attributes: tree density (live trees/ha), tree diameter at breast height (dbh), stem density (live trees + shrubs/ha), snag density (standing dead trees/ha), snag dbh, downed wood density (pieces/ha), and downed wood volume (vol; m^3/ha). The models were composed of random effects associated with the plot and the primary capture occasion and fixed effects associated with the habitat attribute of interest. The 12 primary capture occasions consisted of a categorical variable describing trapping on the 22 study plots in spring (May) and fall (Oct), 2004–2009. For each of the 7 habitat attributes, we evaluated a linear (gray) model and a linear (blue) + quadratic (gold) model. We derived abundance estimates from woodrat encounter histories and capture probabilities estimated from Pollock's robust design mark-recapture analysis in which 3 consecutive trap-nights (secondary capture occasion) were conducted within each primary capture occasion.

Structuring zero-inflated regression models to reflect the BACI experimental design without respect to continuous measures of habitat attributes demonstrated no effect of downed wood removal on plot-level reproduction rate ($\chi^2_2 = 0.236$, $P = 0.901$). Further, we observed no significant association between reproduction rate and any of the 7 habitat attributes that we evaluated (Figure 4A). However, several of the attributes were positively associated with reproductive success (i.e., the presence of ≥1 juveniles within plots in spring; Figure 4B). The model incorporating snag density was the best model describing reproductive success (ΔAIC_c = 2.88 for the next model; Table S4, available in Supporting Information). The zero-inflation portion of this model indicated that on plots with more snags there tended to be at least one juvenile captured during spring capture occasions ($\beta_{\text{snag density}} = -0.926$, SE = 0.271; Figure 4B), but the data did not support an association between snag dbh (an index of snag size; $\beta_{\text{snag dbh}} = 0.553$, SE = 0.299) and reproductive success.

DISCUSSION

Assessment of big-eared woodrat population dynamics within a BACI design demonstrated a complex response of demographic rates to habitat attributes and fuel-reduction practices within an oak woodland in coastal-central California. Our combined observational and experimental results highlight the importance of downed wood and snags for the maintenance of high-quality woodrat habitat (i.e., a resource that produces occupancy; Hall et al. 1997). Amid rapid and ongoing natural and human-caused threats to California's 3 million ha of oak woodland,

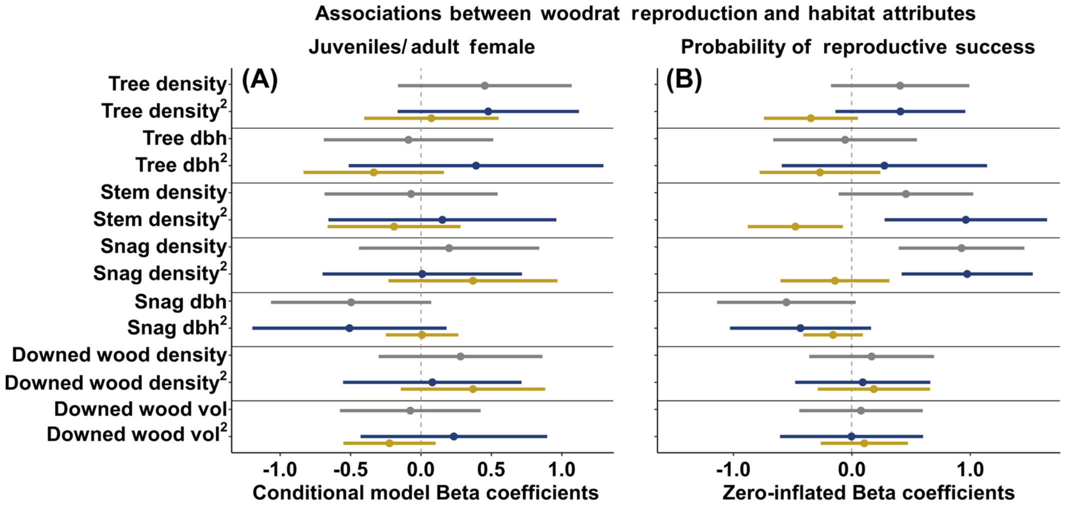

FIGURE 4 Zero-inflated mixed effect model beta coefficients illustrating the associations between big-eared woodrat reproduction during 2004–2009 among 22 1.1-ha study plots on Camp Roberts, California, USA, relative to the following habitat attributes: tree density (live trees/ha), tree diameter at breast height (dbh), stem density (live trees + shrubs/ha), snag density (standing dead trees/ha), snag dbh, downed wood density (pieces/ha), and downed wood volume (vol; m^3/ha). The models were composed of random effects associated with the plot and primary capture occasions represented by 3 consecutive nights of trapping conducted in spring (May), and fixed effects associated with the habitat attribute of interest. We evaluated a linear (gray) model and a linear (blue) + quadratic (gold) model for each habitat attribute. Conditional beta coefficients (A) represent the associations between habitat attributes and reproductive rate (juveniles/adult female captured within a plot in spring), whereas zero-inflated beta coefficients (B) reflect the probability of reproductive success (≥1 juvenile within a plot in spring).

land managers are challenged with balancing the ecological value of coarse woody debris in these ecosystems with the risks of extreme wildfire.

The best predictor of woodrat survival was the volume of downed wood, with survival increasing as volume of wood increased (Figure 2A). We observed an annual survival rate of 40% among treatment plots compared to 47% among control plots, representing an 18% higher survival rate where downed wood was retained. Although a detailed population viability assessment is required to fully determine the impact of such a difference on woodrat population persistence, insight can be drawn from other studies. For example, over 25 years, Getz et al. (2006, 2007) demonstrated that survival rate was the primary driver of meadow vole (*Microtus pennsylvanicus*) population cycles. Indeed, small changes in survival rates contributed to large increases in population density. Getz et al. (2007) surmised that variation in predation pressure was the major factor driving the observed differences in survival rates. Similarly, downed wood on our study area may have provided some protection from generalist predators, thereby contributing to increased survival among plots in which it was retained. During times of environmental stress, the contribution of downed wood to survival could prove important for the persistence of local populations.

In addition to the positive influence of downed wood on woodrat survival, this habitat resource was positively associated with site fidelity. Following the experimental removal of downed wood, woodrat emigration rates averaged 28% on removal plots compared to 17% on the study plots where it was not removed. The 65% difference in emigration rate demonstrates that woodrats were much more likely to remain on plots with abundant downed wood (Figure 2B). This pattern was consistent whether downed wood was quantified by density or volume and for both sexes and juveniles, the cohort that typically disperses. Notably, the quadratic models that described the relationship between downed wood volume and both emigration and woodrat survival were competitive (Tables 1 and 2). The curvilinear relationships between downed wood volume and woodrat emigration and survival indicate that the amount of downed wood observed across study plots spanned a biologically meaningful range of this resource for woodrats. Further, the curvilinear relationships demonstrate that optimal conditions for woodrat survival and site fidelity were observed among plots with intermediate amounts of downed wood. Thus, the model indicates that land managers could remove some downed wood within Camp Roberts without negatively affecting woodrat demographic rates.

Downed wood and snags may contribute to the persistence of a big-eared woodrat population by providing structural support and a more favorable microclimate for houses. Of the 314 pieces of downed wood we sampled at Camp Roberts, 15% either contained a woodrat nest within a hollow or supported a house (Tietje et al. 2015). These patterns have also been observed in other *Neotoma* species (dusky-footed woodrat [Innes et al. 2007] and eastern woodrat [*N. floridana*; Knowles and Burger 2008]). We speculate that nests constructed by woodrats within downed wood hollows and the stick houses that are supported by it have a cooler microclimate. In comparison to thin sticks, coarse wood absorbs and retains more moisture that slowly vaporizes and cools the immediate environment. Such microsite characteristics can help moderate the effects of hot and dry environmental conditions that threaten the diversity of the small mammal community on our study area (Ghimirey et al. 2023).

Downed wood availability did not influence our measures of woodrat reproduction, namely reproductive rate (juveniles/adult female; Figure 4A; Table S4) or reproductive success (presence of juveniles on a plot; Figure 4B). Regarding snags, plot-level snag density was strongly associated with reproductive success, whereas snag dbh (diameter, an index of snag size) was not. This unexpected finding may be explained by the varying relationships among snag size, habitat complexity, and the occurrence of juvenile woodrats. On study plots with many snags, snags were smaller, habitat structure was complex, and we captured more juvenile woodrats in spring. Conversely, on plots where there were few snags, snags were larger, but habitat was not complex, and plots supported fewer woodrats. This suggests that on the more vegetatively complex plots, the smaller snags were used for reproduction, whereas on plots where snags were larger, there were few woodrats to occupy them.

We propose that the positive correlation between snag density and reproductive success was due to the quality of natal nests constructed by females in snags or in hollows within their underlying root structure. Future inquiries into this association may reveal that nests built inside snags support neonate survival by providing greater protection from predators and superior weather-related shelter. The incorporation of motion-sensitive cameras in monitoring efforts would provide a clearer picture of how woodrats use snags and their importance for natal dens. Such information would further clarify the ecological value of retaining snags in fire-prone landscapes. Nevertheless, the failure to identify significant associations between reproduction and most habitat attributes suggests that annual climate variability is a stronger driver of woodrat reproduction in our study area (Tietje et al. 2023).

Downed wood and snags were important habitat attributes at Camp Roberts that contributed to higher reproduction rates, greater survival rates, and lower emigration rates of big-eared woodrats, thereby creating more favorable conditions for occupancy and population persistence. That is, these resources represent important components of high-quality woodrat habitat, as defined by Hall et al. (1997) and Johnson (2007). We expected that woodrat abundance would also be positively associated with greater amounts of coarse woody debris. Rather, woodrat abundance was more strongly associated with other habitat attributes, namely live tree density and stem density (i.e., habitat complexity; Figure 3), which were not strong predictors of survival, emigration, or reproduction (Tables 1, 2, S4; Figure 4). The ideal free distribution theory (Fretwell and Lucas 1969) predicts a higher density of individuals in higher-quality habitat. Therefore, there was a disconnect in our study area between woodrat abundance and habitat quality. Although there are several mechanisms that may be responsible for this phenomenon, it is reasonable to conclude that competitive interactions among individuals played a substantial role. Big-eared woodrats are aggressive, competitive, and at least marginally territorial (Hunter et al. 2017). On our study area, the dominant individuals that occupied areas with more downed wood may have excluded weaker competitors, relegating them to lower-quality patches (an example of an ideal despotic distribution; Fretwell and Lucas 1969). Possibly, the relative dearth of coarse woody debris in California oak woodlands (Tietje et al. 2002) intensifies despotic interactions among individuals. An additional question that remains is whether woodrat behavioral interactions limit abundance within high-quality habitats and if these environs produce net surpluses of young animals that disperse into surrounding areas of lesser quality.

The experimental removal of downed wood in our study area was detrimental to woodrat demographic rates. Consequently, management decisions for California oak woodland should seek to balance the ecological benefits of coarse woody debris with the risk of wildfire. Pertinent insight is provided by a prescribed fire of low to moderate intensity (flame length generally < 1 m) conducted at Camp Roberts. This experimental fire reduced downed wood density by 35%, snag density by 13%, and woodrat houses by 30% (Vreeland and Tietje 1998). Despite these reductions, the only detected effect on the woodrat population was a decrease in the reproduction rate (juveniles/adult female) during late winter and spring following the fire (Lee and Tietje 2005). Based on these findings and our study results, moderate reductions of coarse woody debris can reduce wildfire risk while maintaining high-quality habitat for woodrats and other dependent species.

MANAGEMENT IMPLICATIONS

Big-eared woodrats will benefit from management practices that maintain or increase the availability of downed wood and snags. Measures to enhance these resources, however, must be balanced according to the risk involved. That is, caution needs to be exercised to ensure that these practices do not inadvertently increase wildfire risk. To effectively implement these land management practices, it would be prudent to develop and provide educational programs for California ranchers—the owners and managers of 75% of California oak woodlands.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Handling of animals followed the guidelines of the University of California, Berkeley, Institutional Animal Care and Use Committee (permit R-166) and the guidelines of the American Society of Mammalogists (Sikes et al. 2016).

DATA AVAILABILITY STATEMENT

With the acceptance of this manuscript, we agree to archive the data used in this analysis at Data Dryad so that it may enter into the public domain for future use by fellow scientists and managers.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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Supporting Information

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Table S1. Volume (m^3/ha) and density (pieces/ha) of downed dead wood on treatment and control 1.1-ha study plots on Camp Roberts, California, USA, 2004–2009, that were included in a before-after-control-impact (BACI) study to evaluate the effect of downed dead wood removal on big-eared woodrat demographics. We ordered plots based on the volume of downed wood and sequentially paired plots, with 1 plot from each pairing randomly assigned to the experimental treatment group. All downed wood was removed from the treatment plots between Jan and Mar 2007, the midpoint of the study.

Treatment/control	Downed wood volume (m^3/ha)	Downed wood density (logs/ha)
Treatment 1	21.02	181
Control 1	15.16	337
Treatment 2	13.72	295
Control 2	11.33	348
Treatment 3	8.77	162
Control 3	10.14	207
Treatment 4	8.67	244
Control 4	9.26	171
Treatment 5	7.31	112

Control 5	8.18	154
Treatment 6	6.24	120
Control 6	5.40	79
Treatment 7	7.09	234
Control 7	6.79	174
Treatment 8	5.02	96
Control 8	6.04	109
Treatment 9	4.39	136
Control 9	5.87	125
Treatment 10	2.82	58
Control 10	3.62	123
Treatment 11	2.61	93
Control 11	0.31	27

Table S2. Summary of top 20 Pollock’s robust design models from mark-recapture study investigating big-eared woodrat demographics among 22 1.1-ha study plots established on Camp Roberts, California, USA, 2004–2009. Models were ranked based quasi-Akaike’s Information Criterion corrected for small sample size (QAIC$_c$). Model weights (w_i), model likelihoods, number of parameters, and quasi-deviance scores are also presented. All-combinations of robust design models were evaluated in which survival (S) varied as a function of age (juvenile vs. adult), sex, and primary occasion (a categorical variable describing each of the 12 trapping occasions conducted in May and Oct of 2004–2009). Probability of capture (p) varied as a function of age, sex, and occasion, and temporary emigration (γ'') varied as a function of sex (temporary emigration [γ'] was modeled as an intercept only).

Model	QAIC$_c$	ΔQAIC$_c$	w_i	Model likelihood	Number of parameters	Quasi-deviance
S(age + sex + occasion) γ''(sex) γ'(intercept) p(age + sex + occasion)	24,319.18	0.00	0.27	1.00	30	24,258.90
S(age + sex + occasion) γ''(sex + season) γ'(intercept) p(age + sex + occasion)	24,320.61	1.44	0.13	0.49	31	24,258.32
S(age + sex + occasion) γ''(age) γ'(intercept) p(age + sex + occasion)	24,321.32	2.15	0.09	0.34	29	24,263.07

S(age + sex + occasion) *γ*”(intercept) *γ*’(intercept) *p*(age + sex + occasion)	24,322.14	2.97	0.06	0.23	29	24,263.89
S(age + sex + occasion) *γ*”(sex + age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,322.17	2.99	0.06	0.22	32	24,257.86
S(sex + occasion) *γ*”(sex) *γ*’(intercept) *p*(age + sex + occasion)	24,322.17	3.00	0.06	0.22	28	24,265.93
S(sex + occasion) *γ*”(age) *γ*’(intercept) *p*(age + sex + occasion)	24,322.58	3.40	0.05	0.18	28	24,266.34
S(age + sex + occasion) *γ*”(age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,322.68	3.51	0.05	0.17	30	24,262.41
S(sex + occasion) *γ*”(sex + age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,323.14	3.96	0.04	0.14	31	24,260.85
S(age + sex + occasion) *γ*”(season) *γ*’(intercept) *p*(age + sex + occasion)	24,323.31	4.13	0.09	0.35	30	24,263.03
S(sex + occasion) *γ*”(age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,324.28	5.11	0.02	0.08	29	24,266.03

S(sex + occasion) *γ*’’(sex + season) *γ*’(intercept) *p*(age + sex + occasion)	24,325.35	6.17	0.01	0.05	30	24,265.07
S(sex + occasion) *γ*’’(intercept) *γ*’(intercept) *p*(age + sex + occasion)	24,325.74	6.56	0.01	0.04	27	24,271.52
S(sex + occasion) *γ*’’(season) *γ*’(intercept) *p*(age + sex + occasion)	24,327.17	8.00	0.00	0.02	28	24,270.93
S(age + occasion) *γ*’’(sex + season) *γ*’(intercept) *p*(age + sex + occasion)	24,334.05	14.87	0.00	0.00	30	24,273.78
S(age + sex + occasion) *γ*’’(sex + age) *γ*’(intercept) *p*(age + sex + occasion)	24,335.08	15.90	0.00	0.00	30	24,274.80
S(age + occasion) *γ*’’(sex + age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,335.18	16.00	0.00	0.00	31	24,272.89
S(occasion) *γ*’’(sex + age + season) *γ*’(intercept) *p*(age + sex + occasion)	24,336.20	17.02	0.00	0.00	30	24,275.93
S(age + sex + occasion) *γ*’’(sex + season) *γ*’(intercept) *p*(age + occasion)	24,336.33	17.16	0.00	0.00	30	24,276.06

S(age + sex + occasion) γ''(sex + age) γ'(intercept) *p*(age + sex + occasion)	24,337.10	17.92	0.00	0.00	31	24,274.80

Table S3. Linear mixed effect model rankings based on Akaike's Information Criterion corrected for small sample size (AIC_c), evaluating the association between big-eared woodrat abundance among 22 1.1-ha study plots, established on Camp Roberts, California, USA, 2004–2009, relative to the following habitat attributes: 1) tree density (live trees/ha), 2) tree dbh, 3) stem density (live trees + shrubs/ha), 4) snag density (standing dead trees/ha), 5) snag dbh, 6) downed wood density (pieces/ha), and 7) downed wood volume (vol; m^3/ha). Models were comprised of random effects associated with the plot and trapping occasion (a categorical variable describing each of the 12 primary trapping occasions) and fixed effects associated with the habitat attribute of interest, evaluating both a linear and linear + quadratic effect for each habitat attribute. Abundance estimates were derived from woodrat encounter histories and capture probabilities estimated from Pollock's robust design mark-recapture analyses based on 3-night capture occasions (secondary capture occasions) conducted for each study plot in May and Oct (primary occasions) from 2004–2009.

Model	AICc	ΔAICc	AICc weights (w_i)	Number of parameters
Stem density^{2a}	1,932.73	0	0.99	6
Snag density^{2}	1,944.22	11.49	0	6
Snag density	1,944.24	11.51	0	5
Stem density	1,944.59	11.86	0	5
Tree density	1,947.06	14.33	0	5
Snag dbh^{2}	1,947.33	14.61	0	6

Tree density^2	1,947.55	14.82	0	6
Snag dbh	1,948.7	15.97	0	5
Null (random effect only)	1,949.75	17.02	0	4
Downed wood vol	1,950.87	18.14	0	5
Downed wood vol^2	1,951.31	18.59	0	6
Tree dbh	1,951.35	18.62	0	5
Downed wood density	1,951.82	19.09	0	5
Tree dbh^2	1,953.44	20.71	0	6
Downed wood density^2	1,953.5	20.77	0	6

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[a] Models with a quadratic term (i.e., ^{2}) included both the linear and quadratic representation of the given variable, with only the quadratic variable presented for simplicity (e.g., $N = f$ [stem density+ stem density^2]).

Table S4. Zero-inflated mixed effect model rankings based on Akaike's Information Criterion corrected for small sample size (AIC_c), evaluating the association between big-eared woodrat reproduction (indexed based on the ratio of the number juveniles per adult female) among 22 1.1-ha study plots, established on Camp Roberts, California, USA, 2004–2009, relative to the following habitat attributes: 1) tree density (live trees/ha), 2) tree dbh, 3) stem density (live trees + shrubs/ha), 4) snag density (standing dead trees/ha), 5) snag dbh, 6) downed wood density (pieces/ha), and 7) downed wood volume (vol; m^3/ha). Models were comprised of random effects associated with the plot and primary trapping occasion and fixed effects associated with the habitat attribute of interest, evaluating both a linear and linear + quadratic effect for each habitat attribute. Juvenile and adult female were encountered during 3-night capture occasions (secondary capture occasions) conducted for each study plot in May from 2004–2009 (primary capture occasions; similar trapping efforts conducted in Oct were excluded from analysis as juvenile woodrats are rare in autumn).

Model	AICc	ΔAICc	AICc weights (w_i)	Number of parameters
Snag density	117.12	0	0.7	9
Snag density^{2a}	120	2.88	0.17	11
Snag dbh	122.97	5.85	0.04	9
Snag dbh^2	122.97	5.85	0.04	9
Null (random effect only)	124.57	7.45	0.02	7

Tree density	125.23	8.11	0.01	9
Stem density^2	125.41	8.29	0.01	11
Stem density	126.7	9.58	0.01	9
Tree density^2	126.95	9.83	0.01	11
Downed wood density	127.91	10.78	0	9
Downed wood vol	128.97	11.85	0	9
Tree dbh	129.02	11.9	0	9
Downed wood density^2	129.99	12.87	0	11
Tree dbh^2	131	13.88	0	11
Downed wood vol^2	131.62	14.5	0	11

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[a] Models with a quadratic term (i.e., ^{2}) included both the linear and quadratic representation of the given variable, with only the quadratic variable presented for simplicity (e.g., juveniles/adult female = *f* [Snag density+ Snag density^2]).