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Ideal conditions for increased trapping success of pygmy rabbits (*Brachylagus idahoensis*) across the Great Basin

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Sagebrush-steppe ecosystems are one of the most imperiled ecosystems in North America and many of the species that rely on these habitats are of great conservation concern. Pygmy rabbits (*Brachylagus idahoensis*) are one of these species. They rely on sagebrush year-round for food and cover, and are understudied across their range in the intermountain west due in part to their recalcitrance to standard capture techniques. Identifying an efficient and minimally biased trapping method therefore is a critical first step in learning more about this species. We assessed how trap orientation and weather characteristics influenced trap success for Tomahawk traps placed in and around pygmy rabbit burrows by carrying out trapping surveys at 16 occupied pygmy rabbit sites across the Great Basin from 2016 to 2018. We found that pygmy rabbits had a greater probability of being captured in traps with the open end facing away from burrow entrances. Pygmy rabbits also were more likely to be captured on clear days (0–5% cloud cover) and during periods of cooler temperatures during summer months (June–August). We found no evidence that sex or age ratios differed, or that individuals differed meaningfully, in their preference for certain trap orientations. To increase trap success for pygmy rabbits, we suggest maximizing trapping effort during summer months, at dawn, and maximizing the proportion of Tomahawk traps facing away from burrow entrances. We anticipate that our monitoring protocol will enable more effective research into the ecology and conservation of this cryptic and potentially imperiled species.

Key words: burrowing mammal, capture efficiency, lagomorph, monitoring, sagebrush-steppe

The sagebrush-steppe of western North America, situated largely within the Great Basin geographic region, is one of the most imperiled ecosystems on the continent. Over 50% of sagebrush-steppe ecosystems, which historically covered 63 million ha, have been converted to human land uses or otherwise severely degraded (West 2000; Knick et al. 2003). Furthermore, these habitats continue to be lost and degraded at an alarming rate due to expansion of agriculture, intensive livestock grazing, cheatgrass (*Bromus tectorum*) invasion, altered fire regimes, and encroachment of piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) woodlands (Fleischner 1994; Miller and Rose 1999; Knick et al. 2003; Baker 2006; Pierson et al. 2010).

The loss and degradation of sagebrush habitat is of particular concern for the wildlife species that are completely dependent on sagebrush habitat (hereafter, sagebrush obligates). Within this group of sagebrush obligates are two species, the greater sage-grouse (*Centrocercus urophasianus*), and the pygmy rabbit (*Brachylagus idahoensis*), that consume large quantities of sagebrush year-round (> 50%—Wallestad and Eng 1975; Thines et al. 2004). While the greater sage-grouse has been the target of substantial research funding and conservation interventions, pygmy rabbits remain understudied in almost all aspects of their ecology, particularly population ecology. In 2005 and 2010, pygmy rabbits were denied listing under the Endangered Species Act (ESA), not due to evidence of widespread population stability but, rather, due to insufficient data (USFWS 2005, 2010). Until an effective, standardized population monitoring protocol is available for this species, robust assessment of population dynamics and estimation of extinction risk simply are not possible.

Livetrapping often plays a central role in monitoring wild populations, allowing researchers to undertake capture–mark–recapture studies, genetic sampling, health assessments, and movement/behavior studies. Many different trapping methods have been used over the last 40 years to capture pygmy rabbits in different parts of their range (e.g., spotlighting [Green and Flinders 1979]; using a noose over the burrow entrance [Green and Flinders 1979; Larrucea and Brussard 2007]; Tomahawk

traps near burrow systems, baited with apples [Green and Flinders 1979], canned green beans [Larrucea and Brussard 2007], or with multiple types of bait [Katzner and Parker 1997]; and drift fences [Larrucea and Brussard 2007]). The most successful of these methods rely on visual encounters, and may be biased in the types of individuals that are caught (e.g., individuals that run rather than hide, spend more time away from their burrow system). However, because bait has been shown to be ineffective in increasing trap success (Gahr 1993; Katzner and Parker 1997) and because pygmy rabbits are central-place foragers, spending the majority of their time around their burrow systems (Rosenberg and McKelvey 1999; Heady and Laundré 2005; Camp et al. 2012), traditional trap lines are not practical for capturing a sufficient sample size to undertake meaningful studies.

Due to the decline of sagebrush-steppe habitat and insufficient amount of data on pygmy rabbit population dynamics, it is of increasing importance to study this sagebrush obligate. Identifying an efficient and minimally biased trapping method is a critical first step in learning more about this species. In this study, we assess how trap orientation and weather characteristics influence trap success for Tomahawk traps placed in and around pygmy rabbit burrows (modified trapping grid), and use our results to provide recommendations for optimal trap placement and survey timing. Ultimately, our results will allow researchers to estimate population sizes and monitor population fluctuations more accurately, obtain genetic samples for population and range-wide analyses, and learn more about the basic ecology of this cryptic species.

Materials and Methods

Study areas.—We undertook trapping surveys throughout the Great Basin, focusing on three regions in northeastern, central, and northwestern Nevada, as well as southeastern Oregon, United States. These regions contain some of the largest, contiguous areas of suitable habitat remaining for pygmy rabbits in the southern portion of their range (Smith et al. 2019). Trapping was carried out at 16 sites from late March–August 2016–2018 (Nevada Scientific Collection Permit [SCP] #435057; Oregon SCP #105-16, #087-18; USFWS Special Use Permit #14620-16-015, #14620-17-014, #14620-18-008; Fig. 1). Across trapping sites and years, temperatures ranged from −4.9°C to 6.3°C (mean 0.7°C) in March (n = 1 site), −3.5°C to 16.3°C (mean 6.1°C) in April (n = 5), −1.0°C to 20.2°C (mean 9.5°C) in May (n = 9), 3.5°C to 28.2°C (mean 14.9°C) in June (n = 8), 6.2°C to 34.6°C (mean 21.0°C) in July (n = 11), and 6.3°C to 30.0°C (mean 19.0°C) in August (n = 6). Although it varied by year, March–May generally had high levels of precipitation (range 10.9–73.5 mm; mean 41.3 mm; n = 15) while June–August had low levels of precipitation (range 0–35.9 mm; mean 10.5 mm; n = 25). The size of trapped sites ranged from 45 to 540 ha depending on continuity of sagebrush habitat, level of activity (e.g., number and distribution of fresh fecal pellets and/or pygmy rabbits observed), and burrow density at each site. All trapped sites were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and ranged in elevation from 1,590 to 2,270 m.

Livetrapping and handling.—We classified a site as currently active based on the presence of pygmy rabbit sign (i.e., burrows with fresh pygmy rabbit fecal pellets [Sanchez et al. 2009], 45° crop marks on sagebrush shrubs [Crowell et al. 2018], visual of at least one pygmy rabbit). Once an active site was identified, burrow systems with fresh fecal pellets, multiple entrances, and/or a pygmy rabbit seen nearby, were selected as foci for a clustered sampling design. Each trapping session consisted of 100 single-door Tomahawk live traps (Original Series: Model 201: 41 × 13 × 13 cm, Tomahawk, Wisconsin) and placed within a ca. 10-m radius of the centroid of each focal burrow system. The exact number of traps placed at each burrow system depended on the amount of sign (e.g., fecal pellets, crop marks on sagebrush, visual of a pygmy rabbit) and the number of burrow entrances. At every burrow system, we placed at least one trap in a burrow entrance, usually the largest, facing inward (trap orientation code: BI) and used brown burlap to cover the length of the trap and burrow entrance, leaving the back of the trap open to appear as though the trap was an extension of the burrow system (Fig. 2). Brown burlap was used to disguise and to provide shade and additional concealment cover to the traps. Dirt, rocks, and/or sticks were placed on the edges of the burlap to prevent rabbits pushing out around the sides of the trap. This was the only trap orientation that was removed from the burrow when traps were closed for the day to allow rabbits to continue to use the burrow system. All additional burrow entrances had a trap placed in the burrow, but facing outward (trap orientation code: BO) with burlap and dirt placed over the trap similar to the BI trap (Fig. 2). If a burrow entrance was collapsed, but looked as if it had been used in the past, we placed a BO trap but classified it as a false burrow (trap orientation code: FB; Fig. 2.

Pygmy rabbits are most active during crepuscular periods, with peak activity around sunrise during spring and summer months (Larrucea and Brussard 2009). In addition pygmy rabbits have the potential to become heat stressed when ambient temperatures exceed 25°C (Katzner et al. 1997); therefore, this threshold influenced the times we were able to open and examine traps within those crepuscular periods. When afternoon temperatures were < 25°C, usually in the spring, we opened traps ≥ 1 h before sunset and examined and closed traps ≥ 1 h after dark (mean of 5.5 h per trap per session, ranging 3–7 h). Otherwise (or in addition), we opened traps ≥ 2 h before first light and examined and closed traps ≥ 1 h after sunrise before temperatures reached 25°C (mean of 6 h per trap per session, ranging 4–11 h). The period between opening and closing traps was deemed as one "visit." We recorded temperature (°C) and wind speed (m/s) approximately 2 m above the ground using an anemometer, before opening and closing traps, and used the resulting mean of each measure in our analyses. Cloud cover and precipitation data were classified on an ordinal scale according to the dominant conditions throughout the trapping "visit" (Table 1).

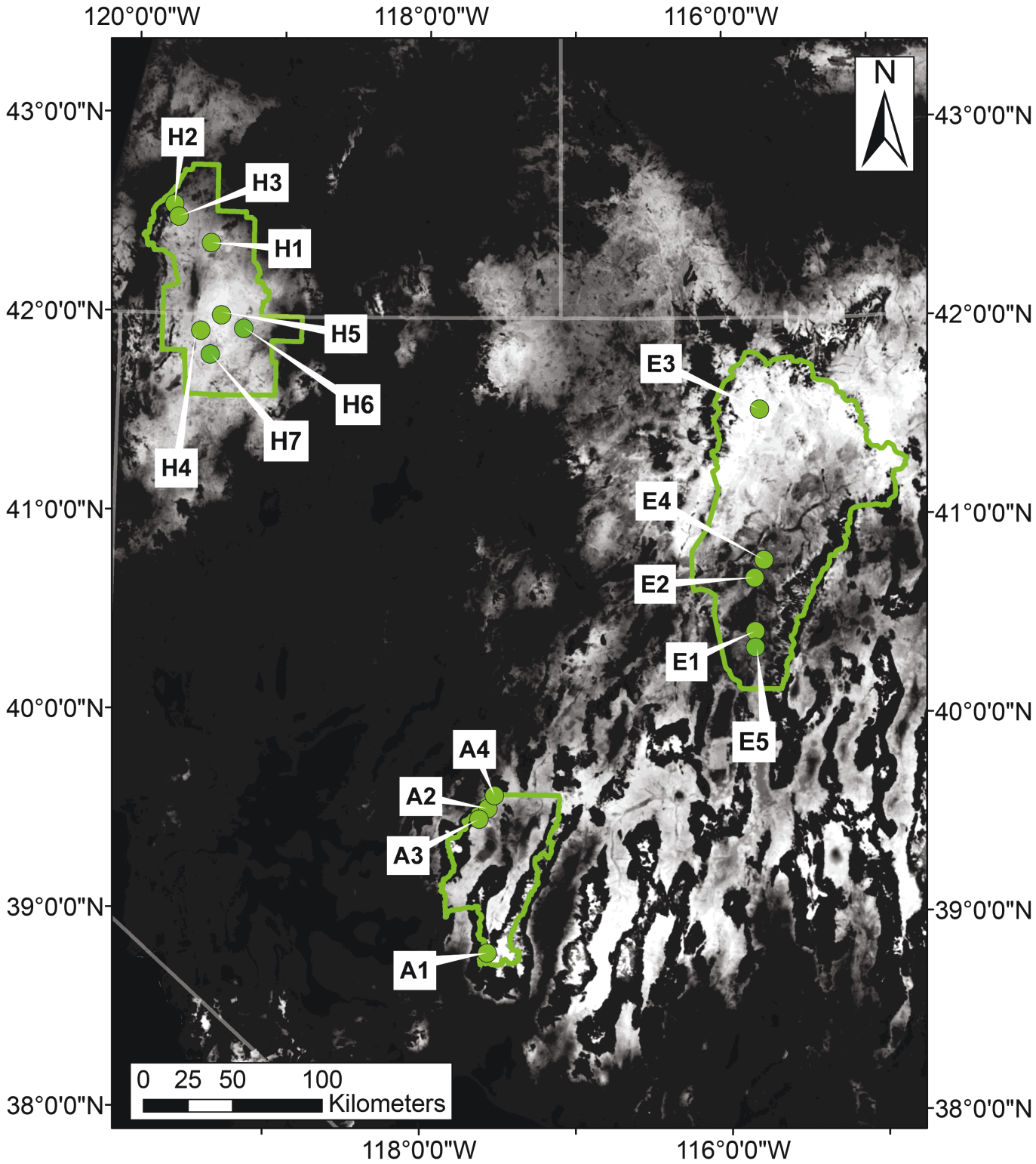

Fig. 1.—Pygmy rabbit (*Brachylagus idahoensis*) trap sites in three regions (green outlines) of the Great Basin. Background shows habitat suitability (K. Zeller, USDA Forest Service, Aldo Leopold Wilderness Research Institute, pers. comm.) ranging from 0.7 (dark gray) to 1.0 (white). Letters correspond to sites in Fig. 6.

Upon capture, pygmy rabbits were transferred to a mesh handling bag and weighed with a 600-g Pesola spring scale to the nearest gram. We determined the sex of each rabbit, their age (based on mass: juvenile < 300 g—Estes-Zumpf and Rachlow 2009), and took a 3-mm diameter ear biopsy punch for DNA analysis. Each new individual was uniquely marked by placing a 9-mm PIT tag (Biomark, Boise, Idaho) subcutaneously between the rabbits' shoulder blades. Other lagomorph

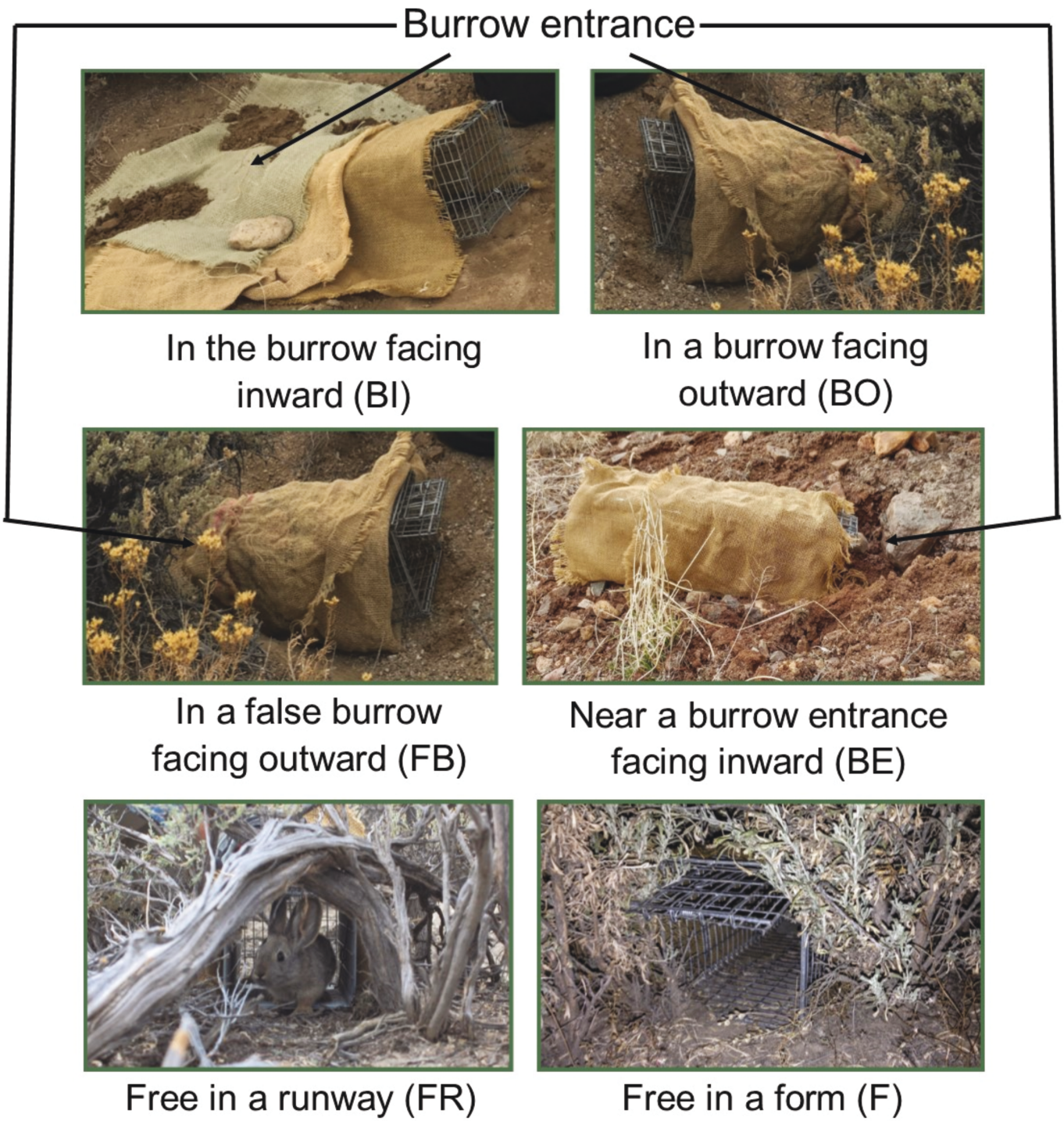

Fig. 2.—The six trap orientations that were placed within a ca. 10-m radius of a central burrow system to trap pygmy rabbits (*Brachylagus idahoensis*) across the Great Basin. Four orientations were placed in or near burrow entrances including in a burrow entrance facing in to catch pygmy rabbits coming out of the burrow (BI), in a burrow entrance facing out to capture pygmy rabbits going into the burrow (BO), in an entrance that had collapsed or a "false burrow" (FB), and near a burrow entrance facing toward the entrance (BE) when entrances were particularly hard to set a trap at. Other trap orientations used away from burrow systems included traps placed in forms where there were many fecal pellets (F), and traps placed in well-used runways (FR).

species were measured and weighed before being released and all nonlagomorph species were released directly from the trap without handling. All livetrapping and handling methods were approved by University of Nevada, Reno Institutional Animal Care and Use Committee (#00643) and followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2016).

Trap success.—To identify ideal trapping conditions and trap configurations for monitoring pygmy rabbits, we investigated capture efficiency as a function of 1) abiotic factors that may

Table 1.—Trap orientation and abiotic variables measured for each trap visit when trapping pygmy rabbits (*Brachylagus idahoensis*). These variables were treated as fixed effects in our generalized linear mixed-effects model ("glmer" function in package lme4—Bates et al. 2015) with captures of pygmy rabbits (1 = capture, 0 = no capture) per trap-night as the response variable and year and trapping site as random variables.

Covariate	Description
Trap orientation	Categorical variable: ranked as one of the following six: BE, near the burrow facing inward; BI, in the burrow facing inward; BO, in the burrow facing outward; F, free in a form; FB, false burrow; FR, free in a runway
Month	Categorical variable: month in which the trapping occurred
Breeding season	Binary variable. 0: nonbreeding season (August to January); 1: breeding season (February to July)
Time of day	Categorical variable: ranked from 1 to 4. 1: traps open around sunrise; 2: traps open around sunset; 3: traps only open during the day; 4: traps only open during the night
Total time open	Continuous variable. Total amount of time traps were open each night
Cloud cover	Categorical variable: ranked from 1 to 4. 1: clear, < 5%; 2: partly cloudy, 5–49%; 3: mostly cloudy, 50–95%; 4: overcast, > 95%
Precipitation	Categorical variable: ranked from 1 to 5. 1: none, 2: light precipitation, 3: rain at times, 4: hail, 5: snow
Adjusted moon illumination (proportion)	Continuous variable. Proportion of the moon that was illuminated multiplied by the proportion of time the moon was above the horizon while traps were open. Proportion moon illumination from 0 (new moon) to 1 (full moon) based on location and date of trapping was obtained from https://www.almanac.com/astronomy/moon/calendar. Time moon was above the horizon calculated using R package suncalc (Agafonkin and Thieurmel 2018)
Mean temperature	Continuous variable. Temperature (°C) was taken immediately before opening and checking traps and averaged. All temperatures were taken with a La Crosse Technology anemometer
Mean windspeed	Continuous variable. Windspeed (m/s) was taken immediately before opening and checking traps and averaged. All windspeed measurements were taken with a La Crosse Technology anemometer

influence trap success and 2) alternative trap orientations (e.g., FR, BO, etc.). We also investigated whether specific trap orientations tended to capture different segments of a pygmy rabbit population (specifically, age and sex) relative to other trap orientations. We fit a generalized linear mixed-effects model ("glmer" function in package lme4—Bates et al. 2015) with trap success as the response variable (1 = pygmy rabbit, 0 = no pygmy rabbit), trap orientation, and abiotic variables, treated as fixed effects (Table 1), and trapping site and year treated as random intercepts. We excluded 15 of 63 trapping sessions for these analyses because one or more abiotic variables were not recorded. We ranked our models using Akaike's information criterion (AIC—Akaike 1981) and constructed partial dependence plots to visualize capture efficiency across the observed range of each predictor variable included in the top model. Prediction uncertainty (95% prediction intervals) for the partial dependence plots was estimated using a bootstrapping procedure (n = 1,000; "bootMer" function in package lme4—Bates et al. 2015). To investigate the effect of trap orientation on trap efficiency, we fit a generalized linear model (glm) with trap success as the response variable, and trap orientation and year as fixed effects. We did not test for trap happiness or trap shyness but we assumed the factors driving capture efficiency for initial captures were the same as those driving capture efficiency for recaptures, and therefore we included all pygmy rabbit captures, recaptures, and captures of individuals not PIT-tagged to fit our models. We used a Tukey post hoc test to conduct pairwise comparisons among trap orientations ("glht" function in package multcomp—Hothorn et al. 2008).

In addition to the capture efficiency of particular trap orientations, we sought to understand if different trap orientations captured different segments of the populations (i.e., whether individuals or population segments differed meaningfully in their preference for certain trap orientations). First, we tested whether sex or age ratios differed by trap orientation using Fisher's exact tests (using only the first capture of each PIT-tagged individual). Further, we performed a Monte Carlo permutation by repeatedly (n = 10,000) scrambling trap orientations within each burrow system, thereby decoupling captures from trap orientation, and compared the observed number of individuals captured exclusively via a single trap orientation (e.g., individuals exclusively captured in BO traps) with the distribution of expected values under the null distribution (no individual-level affinities to a given trap orientation). If an individual was captured more than once in the same trap, we only included the first of those captures to control for unknown factors not related to trap orientation that may have caused an individual to be more likely to be captured in a particular trap (e.g., if an individual's activity was centered around the area of a trap and not because it was a BI trap). We interpreted a test as significant if the observed value was less than the 0.025 quantile or greater than the 0.975 quantile of the null distribution. By conducting the permutation procedure within each burrow system, we were able to account for individuals that may not have been exposed to a particular trap orientation (e.g., if a burrow system did not have any FR traps, then individuals occupying this burrow system would not be expected to be captured in an FR trap).

Finally, because density often is the central metric of interest in monitoring programs, we sought to evaluate the impact of excluding a particular trap orientation on population density estimates. We estimated densities of pygmy rabbits using a spatial capture–recapture (SCR) analysis in a Bayesian framework using JAGS (package R2jags—Su and Yajima 2015). Because BO and FR traps captured more individuals in relation to their availability, we ran our SCR model three times for each site to estimate pygmy rabbit densities 1) with all captures, 2) with captures of all individuals except those captured in BO traps, and 3) with captures of all individuals except those captured in FR traps. We modified our analysis from that of Royle and Gardner (2011) to account for patchy suitable habitat, generally limiting potential activity centers to those 20-m square pixels (based on traps being placed within a 10-m radius of the

burrow system) with known active burrow systems (all other pixels were assigned a small probability of containing unobserved burrow systems, determined on the basis of temporally replicated burrow surveys). We used a minimum convex polygon with a 75-m buffer (rabbits in Idaho were found as far away as 67 m to the nearest burrow system—Camp et al. 2012) around trapped burrow systems to define the study area and supplemented 1,000 simulated individual captures to account for real individuals that may not have been captured and PIT-tagged during our trapping sessions. We ran 1,000 iterations discarding the first 500 as a burn-in. We tested whether the full-data density estimates differed from estimates if we had left out a particular trap orientation by running our SCR model with individuals captured in all trap orientations, a second time excluding all individuals captured in BO traps, and a third time excluding individuals captured in FR traps. We calculated the difference in estimated densities of pygmy rabbits between all captured individuals and excluding individuals captured in BO traps and then the difference between all captured individuals and excluding individuals captured in FR traps. We plotted the mean change in estimated density for each trap orientation that was excluded for 23 sites (eight sites trapped 1 year and five sites trapped for each of 3 years) with 95% confidence intervals. Three sites were excluded from this analysis either because no pygmy rabbits were captured (two sites), or pygmy rabbits only were captured in one trap orientation (one site). All analyses were carried out in R version 3.4.1 (R Core Team 2017) and source code can be found on Github (https://github.com/kevintshoemaker/pygmy_trapping_ms).

Results

Over 3 years, we captured 711 individual pygmy rabbits. Of those individuals, 316 were recaptured at least once throughout the rest of our study. We captured an additional 21 pygmy rabbits that were not tagged because the rabbit escaped or was released due to inclement weather. We had 522 pygmy rabbit captures of 329 individuals in 706 capture events (i.e., captures of any species) over 8,805 trap-nights (i.e., the number of traps open per "visit") in 2016, 419 pygmy rabbit captures (252 individuals) in 504 capture events over 7,445 trap-nights in 2017, and 344 pygmy rabbit captures (189 individuals) in 402 capture events over 14,229 trap-nights in 2018. Number, sex, and age, of individuals captured varied by site, as did the number of recaptured individuals (Table 2). Other animals captured in Tomahawk traps included mountain cottontails (*Sylvilagus nuttallii*), black-tailed jackrabbits (*Lepus californicus*), Ord's kangaroo rats (*Dipodomys ordii*), ground squirrels (*Spermophilus* spp.), least chipmunks (*Tamias minimus*), a sage thrasher (*Oreoscoptes montanus*), and weasels (*Mustela* spp.).

Our top mixed-effects model included trap orientation, cloud cover, month, mean temperature, and the interaction between month and mean temperature, as the most influential variables when trapping pygmy rabbits (Table 3). Pygmy rabbits were less likely to be captured on partly cloudy (5–49%; $P < 0.05$) and overcast days (> 95% cloud cover; $P < 0.001$; Fig. 3A). Mean temperatures recorded during trapping "visits" across all years and study sites ranged 4.2°C to 7.7°C in March ($n = 3$ "visits"), 2.5°C to 18.9°C in April ($n = 37$), 3.4°C to 18.7°C in May ($n = 60$), 0.2°C to 19.8°C in June ($n = 63$), 6.5°C to 22.8°C in July ($n = 72$), and –0.3°C to 19.3°C in August ($n = 51$). As mean temperature increased, probability of capture also increased, although this effect was not significant ($P = 0.81$; Fig. 3C). Pygmy rabbits also were less likely to be captured during the months of April ($P < 0.04$) and May ($P < 0.002$; Fig. 3D). In May and August, pygmy rabbits were

Table 2.—Number of individual pygmy rabbits (*Brachylagus idahoensis*) captured, with number of these individuals recaptured at least once in parentheses, in 2016, 2017, and 2018, broken down by site, age, and sex of adults. Only individuals where age and sex were definitive were included. Five sites were trapped in all 3 years, and 11 sites were trapped for 1 year.

Site	Age	Sex	Year		
			2016	2017	2018
E1	Adult	Male	25 (11)	23 (11)	12 (4)
		Female	27 (12)	11 (2)	10 (6)
	Juvenile		30 (10)	36 (17)	2 (1)
E2	Adult	Male	13 (5)	21 (17)	7 (2)
		Female	22 (9)	11 (4)	6 (3)
	Juvenile		15 (5)	10 (4)	5 (0)
E3	Adult	Male	1 (1)		
		Female	1 (0)		
	Juvenile		0		
E4	Adult	Male	0		
		Female	0		
	Juvenile		7 (4)		
E5	Adult	Male		6 (4)	
		Female		2 (0)	
	Juvenile			0	
A1	Adult	Male	25 (10)	10 (5)	7 (4)
		Female	25 (11)	11 (7)	5 (2)
	Juvenile		26 (8)	18 (7)	9 (5)
A2	Adult	Male	9 (1)	26 (1)	44 (20)
		Female	11 (3)	17 (4)	40 (18)
	Juvenile		0	9 (2)	22 (6)
A3	Adult	Male		3 (3)	
		Female		3 (3)	
	Juvenile			0	
A4	Adult	Male			1 (1)
		Female			6 (2)
	Juvenile				1 (0)
H1	Adult	Male	26 (13)	3 (0)	5 (2)
		Female	13 (5)	4 (2)	6 (4)
	Juvenile		27 (7)	19 (6)	1 (0)
H2	Adult	Male	3 (1)		
		Female	2 (2)		
	Juvenile		9 (2)		
H3	Adult	Male	2 (1)		
		Female	1 (0)		
	Juvenile		3 (1)		
H4	Adult	Male	2 (0)		
		Female	3 (2)		
	Juvenile		3 (0)		
H5	Adult	Male		4 (2)	
		Female		0	
	Juvenile			1 (0)	
H6	Adult	Male		0	
		Female		0	
	Juvenile			0	
H7	Adult	Male		0	
		Female		0	
	Juvenile			0	

Table 3.—Top generalized linear mixed-effects models based on weighted AIC values. Models were used to investigate pygmy rabbit (*Brachylagus idahoensis*) trap success in response to trap orientation, abiotic factors (fixed effects), year, and trapping site (random effects).

Fixed effects	ΔAIC	$AIC_{weighted}$
Trap Orientation + Cloud Cover + Month * Mean Temperature	0	0.9153156
Trap Orientation + Cloud Cover + Month : Mean Temperature	5.529	0.0576718
Trap Orientation + Cloud Cover	7.046	0.0270117
Trap Orientation	27.747	0.0000008

less likely to be captured with an increase in mean temperatures (both $P \leq 0.04$; Fig. 3E).

Pygmy rabbits were more likely to be captured in BO traps ($P < 0.001$) and less likely to be captured in BI traps ($P < 0.001$) than FR traps (Fig. 3B). Although FR traps captured a greater number of pygmy rabbits than BO traps ($n = 585$ versus 571 pygmy rabbits), BO trap orientation was more than twice as efficient in relation to trap-nights, as any other trap orientation ($P < 0.001$ from glm), even in 2018 when trap success was significantly lower than previous years ($P < 0.001$; Fig. 4). In addition, FR traps were significantly more successful than BI traps ($P < 0.001$), with the success of the remaining three trap orientations (BE, F, FB) falling in between the two (Fig. 4). Fisher's test showed that no trap orientation captured a significantly biased sample of individuals by age ($P = 0.22$) or sex ($P = 0.13$). The permutation tests revealed that slightly more individuals were captured only in BO ($P = 0.02$) and FR ($P = 0.03$) traps than would be expected by random chance and that all other trap orientations were consistent with random expectations (Fig. 5). Although the permutation tests showed that some unknown structure in the population may be contributing slightly to individuals being more or less trappable in BO and FR traps, we wanted to see if this had an impact on population densities. Estimated densities across our trapped sites ranged 0.22–30 pygmy rabbits per ha (mean 5.14 pygmy rabbits per ha) when including all individuals captured in all trap orientations. When excluding only individuals captured in BO traps the mean estimated density decreased by 1.29 pygmy rabbits per ha and ranged from a decrease of 19.73 to an increase of 6.81 pygmy rabbits per ha across trapped sites (Fig. 6A). When excluding individuals captured in FR traps the mean estimated density decreased by 0.06 pygmy rabbits per ha and ranged from a decrease of 21.65 to an increase of 11.16 pygmy rabbits per ha (Fig. 6B). Overall, we found no evidence of meaningful bias with respect to different trap orientations capturing a unique subset of the population.

Discussion

Studying the ecology and demography of pygmy rabbits and other cryptic species of conservation concern requires reliable and repeatable trapping methods. Our study suggests that passive trapping for pygmy rabbits using a modified trapping grid focused in and around pygmy rabbit burrows is a promising candidate for range-wide monitoring of this sensitive, data-deficient species. In addition, our analyses revealed that trap orientation, cloud cover, month, and mean temperature all contribute to trap efficiency. These results, in turn, suggest some promising strategies for increasing trap success when deploying Tomahawk traps in a modified trapping grid.

We found that traps placed in the burrow facing outward (BO) were the most successful trap orientation in relation to their availability throughout our study. Pygmy rabbits are central-place foragers and rely on burrow systems year-round, although to a lesser extent during the summer (May–August—Larrucea and Brussard 2007; McMahon et al. 2017; Milling et al. 2018). Although we carried out this study in the summer primarily, BO traps still were more efficient because pygmy rabbits are more active during crepuscular periods (Larrucea and Brussard 2009; Lee et al. 2010; Milling et al. 2017) and likely are using their burrows as refuge from predators in between bouts of foraging or as thermal refuge during the coldest time of day (i.e., dawn). However, FR traps also caught a greater proportion of rabbits than expected by random, suggesting that these traps still are important to include in a modified trapping grid to maximize capture success of pygmy rabbits. Summer in the Great Basin is characterized by warm temperatures during the day, sometimes exceeding 37°C, and cool temperatures at night, sometimes below 0°C, which may cause small mammals to seek warmer refuges at night and sunrise, the coldest times of day. In summer, pygmy rabbits avoid burrow systems during the day when soil temperatures of resting spots in the shade are warmer than burrow temperatures, but at dawn, when burrow temperatures are warmer than ambient and top-soil temperatures (Milling et al. 2018), we may have captured pygmy rabbits retreating to their burrow systems in search of a thermal refuge. This may explain why we caught a greater proportion of rabbits going into burrow systems (BO traps) than rabbits coming out of burrow systems (BI traps). During the breeding season, pygmy rabbits have larger home ranges, use a greater number of burrow systems, and switch among these burrow systems more often (Gahr 1993; Burak 2006; Sanchez and Rachlow 2008). At dawn, when rabbits are more active and likely exhibit increased movement between burrow systems, they may be captured more readily in FR traps that surround a central burrow system. Although trap efficiency varied among years for BO, FB, and FR traps, the comparative success of trap orientation remained similar over the duration of the study suggesting that pygmy rabbits are not significantly altering their behavior or activity patterns that lead to them being captured between years. This consistency in pygmy rabbit behavior leads us to suggest maximizing BO traps by trapping a greater number of active burrow systems, but still including FR traps to a lesser degree, to capture individuals moving among burrow systems. In this study we used single-door Tomahawk traps because of availability and greater overall success with other small mammals in our research group. However, using double-door traps would eliminate the need to distinguish between BI and BO trap orientations and would presumably capture rabbits entering or exiting the burrow system from any entrance.

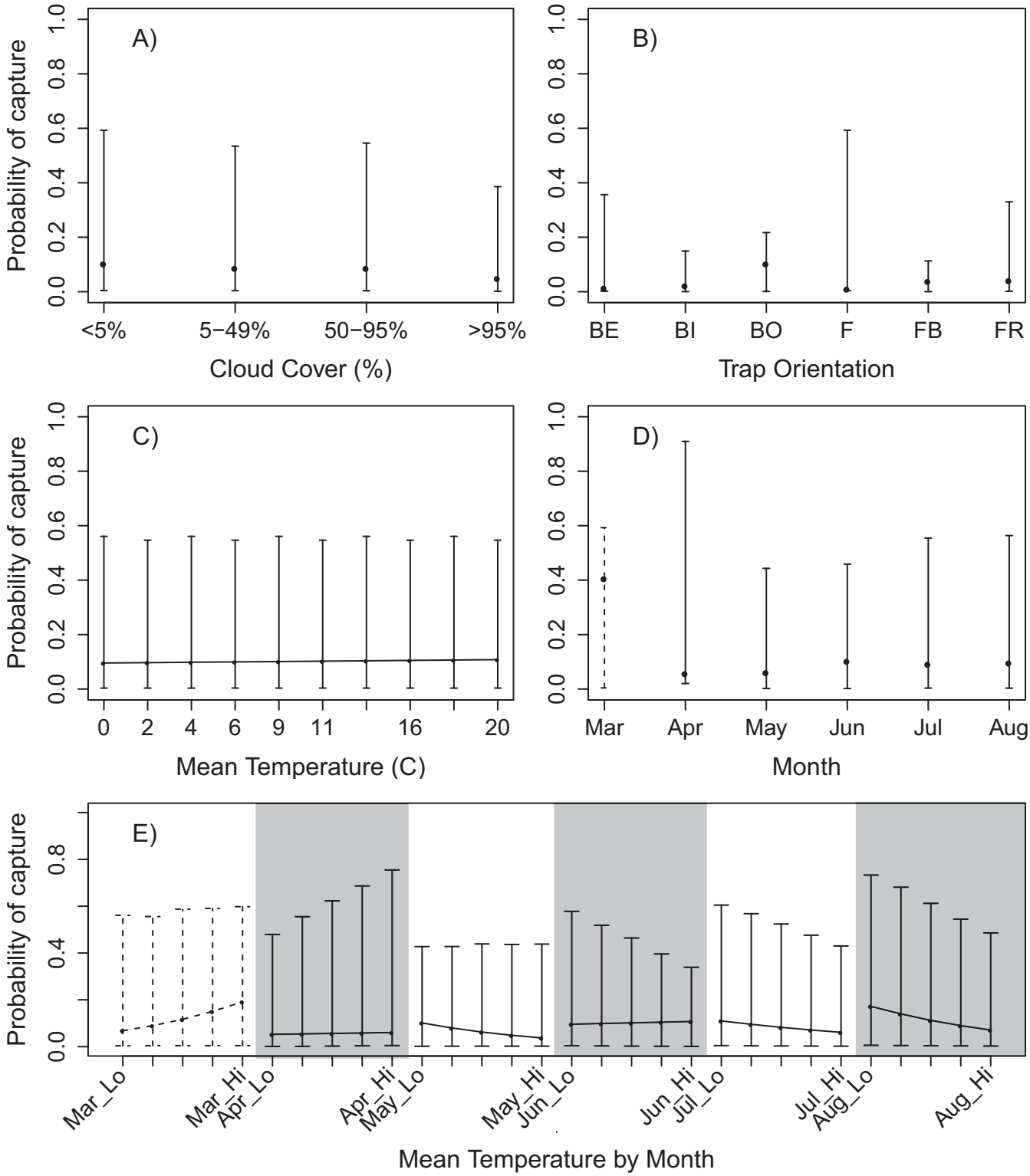

Fig. 3.—Predicted probability of capture when trapping pygmy rabbits (*Brachylagus idahoensis*) across a range of observed conditions at our trapped sites across the Great Basin. Our top generalized linear mixed-effects model included cloud cover (A), trap orientation (B), mean temperature (C), month (D), and the interaction between mean temperature and month (E). The bars represent 95% bootstrap prediction intervals.

Likewise, double-door traps in runways would capture individuals approaching from either direction of the runway.

Although there is no documentation of using our method of placing traps in burrows facing outward to appear as an extension of the burrow, some have used BI-equivalent trap orientations successfully (Sargeant 1966; Connior and Risch 2009). In addition, placing traps around burrow systems rather than in a traditional trapping grid has shown greater capture

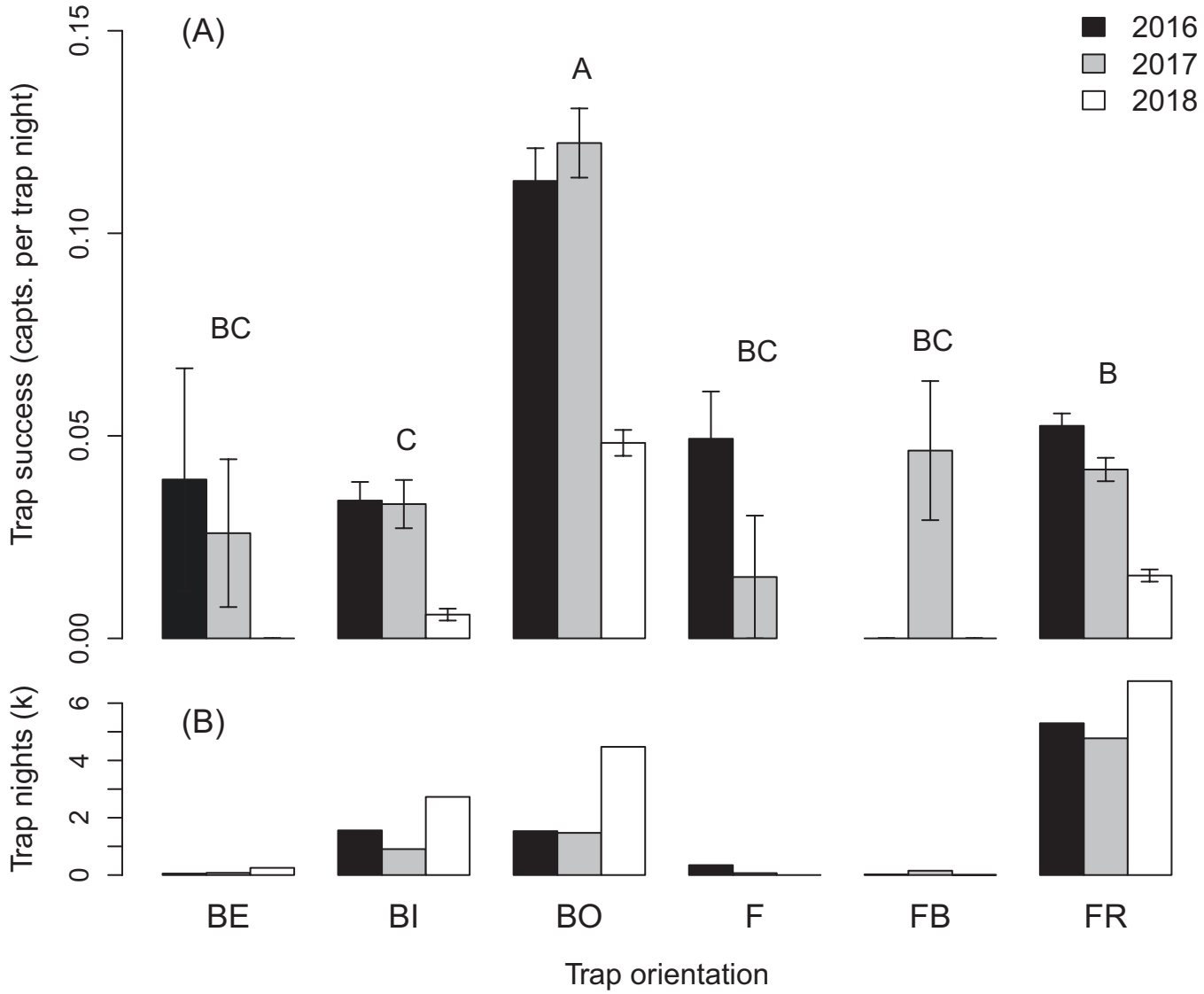

Fig. 4.—We fit a generalized linear model (glm) with trap success as the response variable, and trap orientation (six orientations: four in or near burrow entrances—BE, BI, BO, FB—and two within 10 m of the burrow system—F, FR) and year (2016–2018) as fixed effects. We used a Tukey post hoc test to conduct pairwise comparisons among trap orientations and years. We visualized the proportion of trap success per "visit" (i.e., the period between opening and closing traps) and signified the differential success of trap orientations (Tukey test) with letters (A). Trap-nights (i.e., number of traps open per "visit") are reported as a factor of 1,000 (B).

success with other burrowing small mammal species (Melchior and Iwen 1965). European rabbits (*Oryctolagus cuniculus*) have been found to have a female sex bias when trapping around the entrances to warrens and a male sex bias when trapping away from the warrens, which contrasts our study that found no sex bias in trap efficiency among trap types. Similar to our study though, these trapping methods for European rabbits revealed no significant effect in relation to age structure (Smith et al. 1995). Our study was carried out largely during the breeding season, when both sexes exhibit higher levels of activity (Sanchez and Rachlow 2008; Milling et al. 2017), and juveniles are beginning to disperse (Estes-Zumpf and Rachlow 2009). However, all sexes and ages are susceptible to predation and colder temperatures at dawn and likely use burrow systems as a refuge equally. The lack of sex or age bias in our trapping methods is consistent with other studies that have found 1:1 sex and age ratios in pygmy rabbit populations (Wilde 1978; Gahr 1993) and will be beneficial for future studies that require unbiased trapping methods and an even sex and/or age ratio in relation to abundance in the population. In addition, we found that only BO and FR traps performed slightly better than random when capturing a subset of individuals in a population, although this pattern had no effect on overall population estimates.

Cloud cover also was predicted to contribute to increased pygmy rabbit trap success, with clear skies associated with greater trap success relative to intermediate cloud cover. Increased cloud cover holds in heat during the night and may have decreased the range of temperatures observed and potentially increased mean temperature measured during the

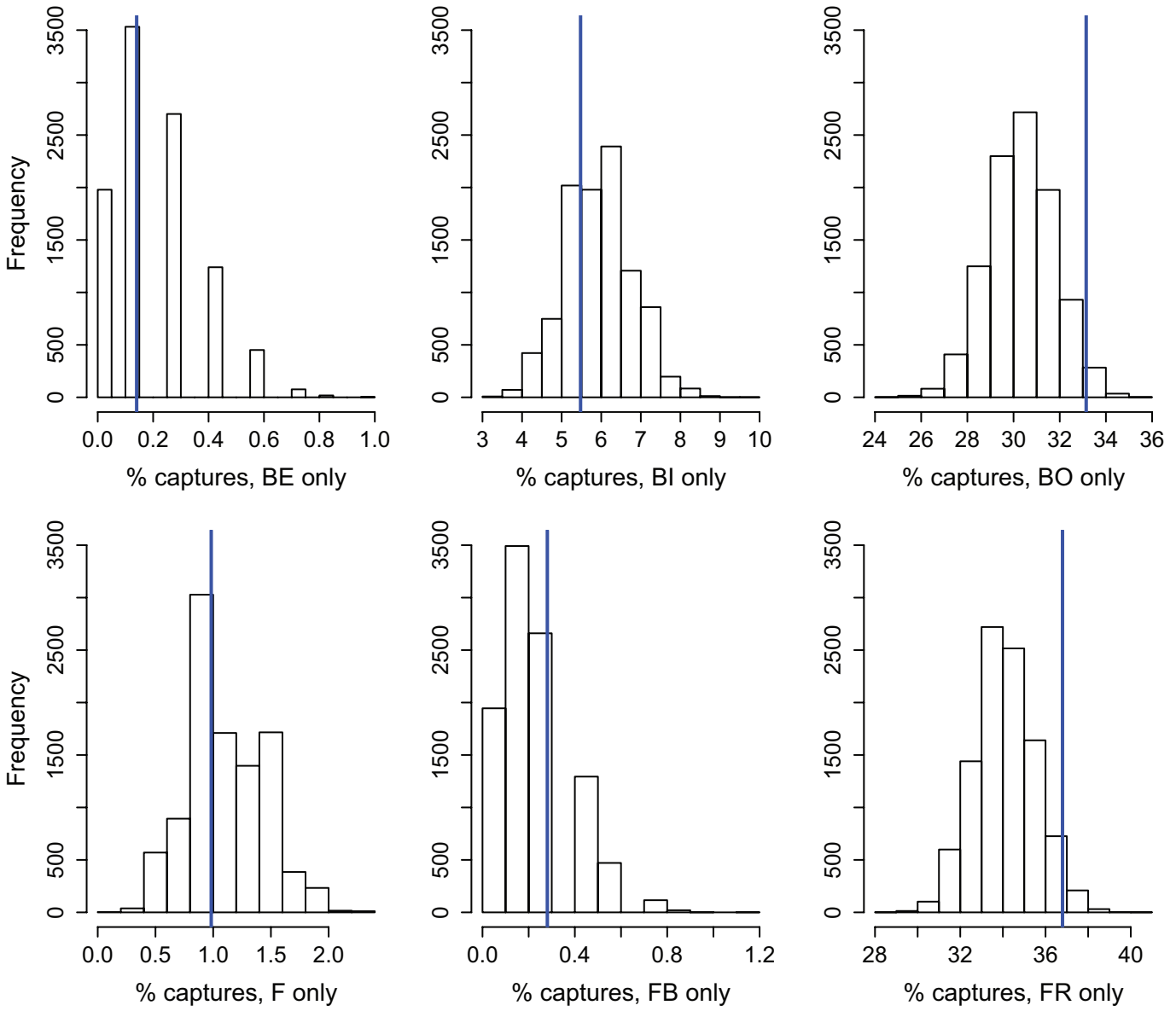

Fig. 5.—Permutation tests (n = 10,000 permutations) were performed by taking individual pygmy rabbits (*Brachylagus idahoensis*) captured by only one trap orientation at a given burrow system and randomizing the trap orientation they could have been captured in to obtain the distribution of expected percent of total captures where individuals were captured exclusively in each trap orientation. The observed percent of total captures where individuals were captured exclusively in each trap orientation is represented by the blue lines.

period our traps were open. Clear skies therefore were associated with cooler temperatures, which would be more likely to drive pygmy rabbits into burrows in search of warmer refuges, thereby increasing trap success. Increasing cloud cover also decreases the amount of light during the night and even during the day, which may reduce predation by predators that depend on sight as a primary means of locating their prey. Alternatively, clear skies may have higher light contrast between open and shaded areas resulting in pygmy rabbits being able to hide more easily without being detected. Other studies have shown contrasting results on the impact of cloud cover on small mammal trap success with some species showing an increase in capture efficiency (prairie voles [*Microtus ochrogaster*] and cotton rats [*Sigmodon hispidus*]—Stokes et al. 2001), and some species showing a decrease in capture efficiency with decreasing cloud cover (northern short-tailed shrew [*Blarina brevicauda*]—Getz 1961; gray squirrel [*Sciurus carolinensis*]—Perry et al. 1977). This suggests the relationship between cloud cover and capture efficiency may be context-specific.

Mean temperature, month, and the interaction between these two variables, also were important in capture efficiency when trapping pygmy rabbits. Other than March, we were most likely to catch an increased number of pygmy rabbits during the summer months (June, July, and August), likely because of greater mean temperatures. Although our results also suggest that we are more likely to catch rabbits in March, we only trapped 1 week in March throughout the 3 years our

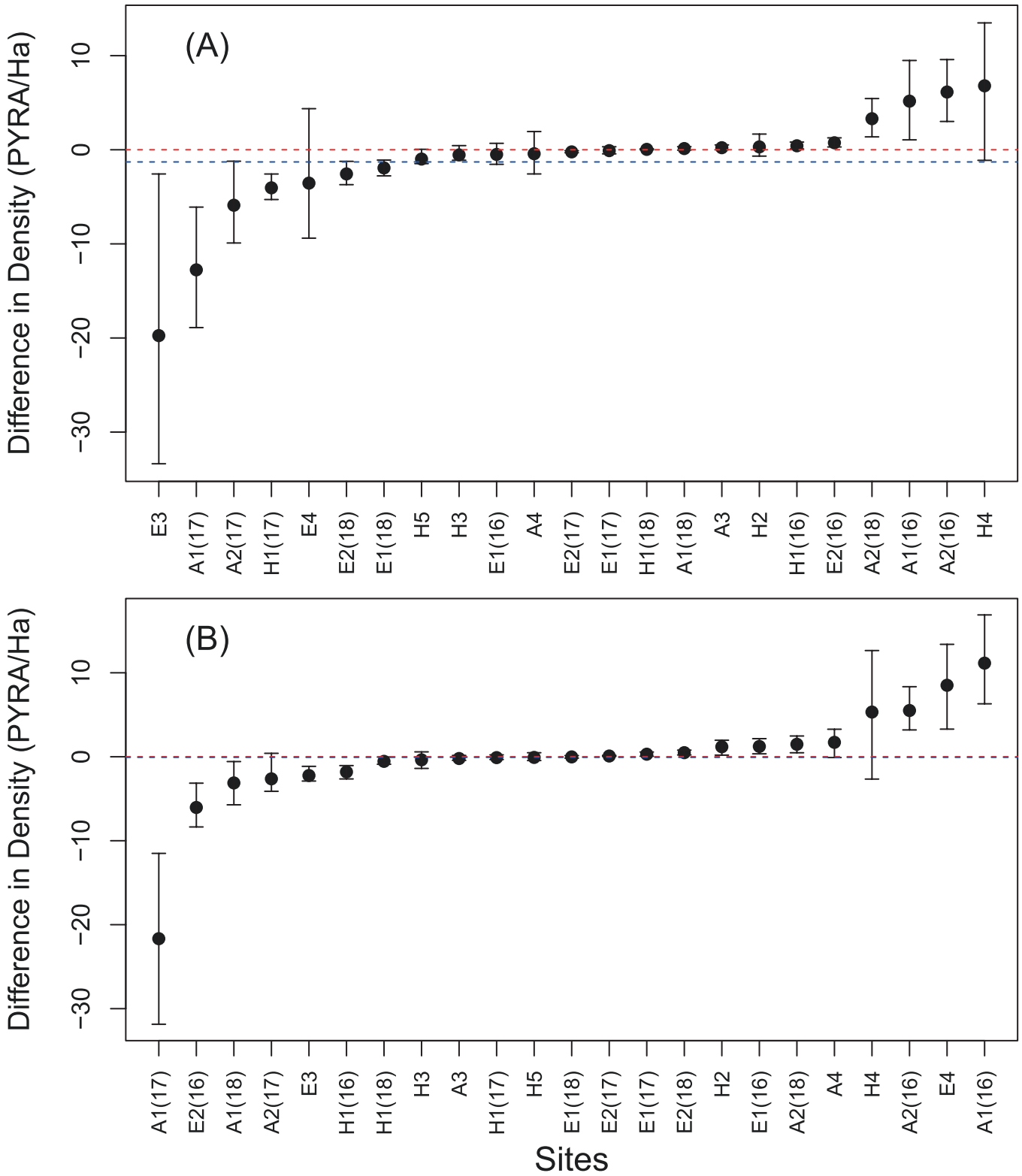

Fig. 6.—Differences in estimated densities (pygmy rabbits [*Brachylagus idahoensis*] per ha) when excluding individuals captured in BO traps (in a burrow entrance facing out; A), or excluding individuals captured in FR traps (in a well-used runway; B). The blue lines are the mean differences in density of all sites. The red lines represent if there was no mean change in difference in density of all sites. Sites on the x-axis correspond to labeled sites in Fig. 1 and numbers in the parentheses refer to the year that site was trapped (2016–2018) if the site was trapped for more than 1 year.

study was carried out, so those results are not completely reliable. While other studies have found ambient temperature does not play a significant role in activity during the summer (Milling et al. 2017), we likely see a greater probability of capture when temperatures are warmer in characteristically cooler months, and when temperatures are cooler in characteristically warmer months, because these temperatures are approaching the lower critical threshold of the thermal neutral zone (Katzner et al. 1997; Milling et al. 2018), allowing them to be more active when thermoregulatory costs are low (Humphries and Careau 2011). This concurs with studies that have found pygmy rabbits are more active at dusk during winter when temperatures are warmer relative to dawn, and more active at dawn during the summer when temperatures are cooler relative to dusk (Larrucea and Brussard 2009; Lee et al. 2010). Similarly, meadow voles (*Microtus pennsylvanicus*) have been shown to alter activity patterns when temperatures reach above 20°C during the day, favoring nocturnal and crepuscular activity over diurnal activity (Getz 1961). In addition, in the spring (April, May) there usually is greater weather variation, including increased precipitation and colder temperatures, that likely drives pygmy rabbits to be in their burrows longer, even possibly longer than our traps were open. In June, July, and August, temperatures are warming and weather conditions tend to be more consistent and stable, which may equate to an increase in movement and longer periods of activity. Winter trapping has proven to be more effective in previous studies because active burrow systems are easier to identify from fecal pellets on top of the snow and fresh tracks (Price and Rachlow 2011; DeMay et al. 2015). Further, baiting traps may be more effective in winter due to a lack of naturally occurring forbs and grasses (Green and Flinders 1979). However, many remote sites are difficult to access in winter; additional cover or more frequent checking of traps is necessary to ensure animal safety; and finally, adults and young of the year often are indistinguishable from one another during the winter (Estes-Zumpf and Rachlow 2009; DeMay et al. 2016). In addition, pygmy rabbits tend to exhibit higher levels of activity in summer than winter (Larrucea and Brussard 2009; Milling et al. 2017), which likely increases sample size when using our method of trapping in summer months.

The results of our study lead us to suggest placing traps wrapped in burlap in burrow entrances and in well-used runways. Although we did not test the capture efficiency of double-door Tomahawk traps in this study, it may be prudent to explore this option further. In addition, we suggest trapping during summer months (June–August) with traps being opened 2–3 h before dawn and closed 2–3 h after dawn to capture the period when temperatures are cooler and pygmy rabbits most active. Finally, while it is unrealistic to trap only when skies are clear, if the weather becomes overcast during a trapping "visit," we suggest adding additional trapping effort during that trapping session. By following these methods, we can ensure a nonbiased sample of the population and even sex and age ratios in relation to their presence in the population. Pygmy rabbit population dynamics remain relatively unknown across their range and this method of trapping, as well as the ideal conditions under which it should be undertaken, will assist researchers and managers in capturing larger sample sizes and monitoring populations more effectively to learn more about this understudied, cryptic species.

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Literature Cited

Agafonkin, V., and B. Thieurmel. 2018. Suncalc: compute sun position, sunlight phases, moon position and lunar phase. R package version 0.4. https://CRAN.R-project.org/package=suncalc. Accessed 17 October 2018.

Akaike, H. 1981. Likelihood of a model and information criteria. Journal of Econometrics 16:3–14.

Baker, W. L. 2006. Fire and restoration of sagebrush ecosystems. Wildlife Society Bulletin 34:177–185.

Bates, D., M. Mäechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Burak, G. S. 2006. Home ranges, movements, and multi-scale habitat use of pygmy rabbits (*Brachylagus idahoensis*) in southwestern Idaho. M.S. Thesis, Boise State University. Boise, Idaho.

Camp, M. J., J. L. Rachlow, B. A. Woods, T. R. Johnson, and L. A. Shipley. 2012. When to run and when to hide: the influence of concealment, visibility, and proximity to refugia on perceptions of risk. Ethology 118:1010–1017.

Connior, M. B., and T. S. Risch. 2009. Live trap for pocket gophers. Southwestern Naturalist 54:100–104.

Crowell, M. M., L. A. Shipley, J. S. Forbey, J. L. Rachlow, and R. G. Kelsey. 2018. Dietary partitioning of toxic leaves and fibrous stems differs between sympatric specialist and generalist mammalian herbivores. Journal of Mammalogy 99:565–577.

DeMay, S. M., P. A. Becker, L. P. Waits, T. R. Johnson, and J. L. Rachlow. 2016. Consequences for conservation: population density and genetic effects on reproduction of an endangered lagomorph. Ecological Applications 26:784–795.

DeMay, S. M., J. L. Rachlow, L. P. Waits, and P. A. Becker. 2015. Comparing telemetry and fecal DNA sampling methods to quantify

survival and dispersal of juvenile pygmy rabbits. Wildlife Society Bulletin 39:413–421.

Estes-Zumpf, W. A., and J. L. Rachlow. 2009. Natal dispersal by pygmy rabbits (*Brachylagus idahoensis*). Journal of Mammalogy 90:363–372.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629–644.

Gahr, M. L. 1993. Natural history, burrow habitat and use, and home range of the pygmy rabbit (*Brachylagus idahoensis*) of Sagebrush Flat, Washington. M.S. Thesis, University of Washington. Seattle, Washington.

Getz, L. L. 1961. Responses of small mammals to live-traps and weather conditions. American Midland Naturalist 66:160–170.

Green, J. S., and J. T. Flinders. 1979. Techniques for capturing pygmy rabbits. The Murrelet 60:112–113.

Heady, L. T., and J. W. Laundré. 2005. Habitat use patterns within the home range of pygmy rabbits (*Brachylagus idahoensis*) in southeastern Idaho. Western North American Naturalist 65:490–500.

Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models. Biometrical Journal 50:346–363.

Humphries, M. M., and V. Careau. 2011. Heat for nothing or activity for free? Evidence and implications of activity-thermoregulatory heat substitution. Integrative and Comparative Biology 51:419–431.

Katzner, T. E., and K. L. Parker. 1997. Vegetative characteristics and size of home ranges used by pygmy rabbits (*Brachylagus idahoensis*). Journal of Mammalogy 78:1063–1072.

Katzner, T. E., K. L. Parker, and H. H. Harlow. 1997. Metabolism and thermal response in winter-acclimatized pygmy rabbits (*Brachylagus idahoensis*). Journal of Mammalogy 78:1053–1062.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. M. Vander Haegen, and C. van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105:611–634.

Larrucea, E. S., and P. F. Brussard. 2007. A method for capturing pygmy rabbits in summer. Journal of Wildlife Management 71:1016–1018.

Larrucea, E. S., and P. F. Brussard. 2009. Diel and seasonal activity patterns of pygmy rabbits (*Brachylagus idahoensis*). Journal of Mammalogy 90:1176–1183.

Lee, J. E., R. T. Larsen, J. T. Flinders, and D. L. Eggett. 2010. Daily and seasonal patterns of activity at pygmy rabbit burrows in Utah. Western North American Naturalist 70:189–197.

McMahon, L. A., J. L. Rachlow, L. A. Shipley, J. S. Forbey, and T. R. Johnson. 2017. Habitat selection differs across hierarchical behaviors: selection of patches and intensity of patch use. Ecosphere 8:e01993.

Melchior, H. R., and F. A. Iwen. 1965. Trapping, restraining, and marking arctic ground squirrels for behavioral observations. Journal of Wildlife Management 29:671–678.

Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52:550–559.

Milling, C. R., J. L. Rachlow, T. R. Johnson, J. S. Forbey, and L. A. Shipley. 2017. Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal. Behavioral Ecology 28:1236–1247.

Milling, C. R., et al. 2018. Seasonal temperature acclimatization in a semi-fossorial mammal and the role of burrows as thermal refuge. PeerJ 6:e4511.

Perry, H. R., Jr., G. B. Pardue, F. S. Barkalow, Jr., and R. J. Monroe. 1977. Factors affecting trap responses of the gray squirrel. Journal of Wildlife Management 41:135–143.

Pierson, F. B. C. J. Williams, P. R. Kormos, S. P. Hardegree, P. E. Clark, and B. M. Rau. 2010. Hydrologic vulnerability of sagebrush steppe following pinyon and juniper encroachment. Rangeland Ecology and Management 63:614–629.

Price, A. J., and J. L. Rachlow. 2011. Development of an index of abundance for pygmy rabbit populations. Journal of Wildlife Management 75:929–937.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/. Accessed 9 December 2019.

Rosenberg, D. K., and K. S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63:1028–1038.

Royle, J. A., and B. Gardner. 2011. Hierarchical spatial capture-recapture models for estimating density from trapping arrays. Pp. 163–190 in Camera traps in animal ecology: methods and analyses (A. F. O'Connell, J. D. Nichols, and K. U. Karanth, eds.). Springer. New York.

Sanchez, D. M., and J. L. Rachlow. 2008. Spatio-temporal factors shaping diurnal space use by pygmy rabbits. Journal of Wildlife Management 72:1304–1310.

Sanchez, D. M., J. L. Rachlow, A. P. Robinson, and T. R. Johnson. 2009. Survey indicators for pygmy rabbits: temporal trends of burrow systems and pellets. Western North American Naturalist 69:426–436.

Sargeant, A. B. 1966. A live trap for pocket gophers. Journal of Mammalogy 47:729–731.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smith, G. C., B. Pugh, and R. C. Trout. 1995. Age and sex bias in samples of wild rabbits, *Oryctolagus cuniculus*, from wild populations in southern England. New Zealand Journal of Zoology 22:115–121.

Smith, I. T., J. L. Rachlow, L. K. Svancara, L. A. McMahon, and S. J. Knetter. 2019. Habitat specialists as conservation umbrellas: do areas managed for greater sage-grouse also protect pygmy rabbits? Ecosphere 10:e02827.

Stokes, M. K., N. A. Slade, and S. M. Blair. 2001. Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. Canadian Journal of Zoology 79:966–972.

Su, Y., and M. Yajima. 2015. R2jags: using R to run "JAGS." R package version 0.5-7. https://CRAN.R-project.org/package=R2jags. Accessed 3 September 2018.

Thines, N. J. S., L. A. Shipley, and R. D. Sayler. 2004. Effects of cattle grazing on ecology and habitat of Columbia Basin pygmy rabbits (*Brachylagus idahoensis*). Biological Conservation 119:525–534.

United States Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants; 90-day finding on a petition to list the pygmy rabbit as threatened or endangered. Federal Register 70:29253–29265.

UNITED STATES FISH AND WILDLIFE SERVICE. 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the pygmy rabbit as endangered or threatened; proposed rule. Federal Register 75:60516–60561.

WALLESTAD, R., AND R. L. ENG. 1975. Foods of adult sage grouse in central Montana. Journal of Wildlife Management 39:628–630.

WEST, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pp. 15–26 in Proceeding of the sagebrush steppe ecosystems symposium, Boise State University, Boise, Idaho, 21–23 June 1999 (P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof, compilers). United States Department of the Interior, Bureau of Land Management, Idaho State Office. Boise, Idaho.

WILDE, D. B. 1978. A population analysis of the pygmy rabbit (*Sylvilagus idahoensis*) on the INEL site. Ph.D. dissertation, Idaho State University. Pocatello, Idaho.

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