Response of a remnant marmot population to habitat enhancement yields insights into marmot ecology

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We evaluated the response of a remnant population of yellow-bellied marmots (*Marmota flaviventris*) to targeted habitat enhancement in an ecological system that had been degraded during ~100 years of intensive livestock management, including marmot eradication. We used capture-recapture data and a novel use of a multistate framework to evaluate geographic expansion of the marmot population pre- and post-habitat enhancement. We also estimated age-structured survival, reproduction, and sex ratios. The marmot population appeared to respond positively to new habitat opportunities created by habitat enhancement: the number of marmots captured increased from three marmots pre-habitat enhancement to 54 (28 adults and yearlings, 26 young) post-habitat enhancement at the end of the study. Marmots expanded geographically by transitioning into habitat-enhanced areas, and adult females occupied and reproduced in all habitat-enhanced areas. The sex ratio of the young population in 2019 was strongly female-biased, which may have been influenced by poor body condition of breeding females owing to unusually prolonged snow cover that year. Adult and yearling survival were within the range of that reported for colonial adults and yearlings in Colorado. Our results suggest that active habitat enhancement can assist in the recovery of marmot populations in systems where marmots historically existed.

Key words: conservation, demography, habitat transition, Montana, multistate models, restoration, sex ratio

Degraded, fragmented, and damaged ecosystems resulting from human-altered landscapes threaten biodiversity worldwide (Sala et al. 2000; Wilson et al. 2016). Assisting in the recovery of such ecosystems is the foundation of ecological restoration (SER 2004), a rapidly developing field of research (Wortley et al. 2013). Increasingly, studies of ecological restoration are incorporating measures of wildlife response, which is essential to evaluating the efficacy and value of restoration efforts (Miller and Hobbs 2007; Suding 2011; Vesk et al. 2015). For example, recent studies have evaluated the response of small mammals (Smith and Gehrt 2010; Larsen et al. 2016), snowshoe hares (Kumar et al. 2018), and large mammals (Stokes et al. 2011) to forest system restoration, as well as small mammal response to grassland system restoration (Mulligan et al. 2013; Mérő et al. 2015), riparian system restoration (Golet et al. 2011), and desert scrub system restoration (Patten 1997).

Ecological restoration aimed at reestablishing ecosystem processes by increasing a specific wildlife population, whose members have been eliminated or have drastically declined, often involves species reintroduction efforts (e.g., wolf reintroduction in Yellowstone National Park; Gunnison's prairie dogs [*Cynomys gunnisoni*] in New Mexico—Davidson et al. 2018), and is beginning to include habitat enhancement singularly targeted for the species of interest. For example, particular native shrubs (e.g., seacoast marsh elder, *Iva imbricata* Walter) were planted expressly to enhance habitat for the endangered Perdido Key beach mouse (*Peromyscus polionotus trissyllepsis*) in Florida after the species' habitat was damaged by storms (Stoddard et al. 2019). In Hungary, Russian olive trees (*Elaeagnus angustifolia*) and certain scrub species were removed to enrich habitat for the vulnerable European ground squirrel (*Spermophilus citellus*—Kenyeres et al. 2018).

For our study, we implemented targeted habitat enhancement for a population of yellow-bellied marmots that had been decimated due to human impact, and measured marmot response pre- and post-habitat enhancement. Although yellow-bellied

marmots are not listed as endangered or threatened, local colonies of marmots that have been persecuted over long periods can all but disappear, resulting in degraded ecosystems. Yellow-bellied marmots are important to the stability of ecological communities of which they are a part because they are prey for numerous predator species, including coyotes (*Canis latrans*), raptors, American martens (*Martes americanus*), long-tailed weasels (*Mustela frenata*), red foxes (*Vulpes vulpes*), and American black bears (*Ursus americanus*—Van Vuren 1991, 2001; Harrison et al. 2019).

Yellow-bellied marmots have been the focus of previous research, revealing important insights into marmot population demography (Oli and Armitage 2004; Ozgul et al. 2007; Borrego et al. 2008), sociality and matrilines (Armitage 1984; Armitage 2013), antipredator behaviors (Blumstein et al. 2009), and communication (Blumstein and Récapet 2009). However, the response of a remnant marmot colony to habitat enhancement remains to be evaluated. As landscape management shifts away from intensive resource extraction toward ecologically sustainable resourcing and restoring ecological processes, understanding how to restore local populations of previously diminished wildlife, such as marmots or prairie dogs, will become increasingly important. Moreover, demonstrating that the response of a marmot population to habitat enhancement can be quantified and rigorously analyzed is important to marmot conservation and broadly relevant to mammal conservation, restoration, and research.

Restoring ecological processes has been a broad objective of our work, as the landscape that the marmot colony of interest occupies (MPG Ranch) is a conservation landscape that has been undergoing ecological restoration, and the focus of restoration research, starting in 2009 (Lekberg et al. 2013; Herget et al. 2015; Mummey and Ramsey 2017). Although marmots historically occupied an area called Woodchuck Creek on MPG Ranch, as evidenced by Salish place names and oral traditions documented by Malouf (1974), marmots had all but disappeared from MPG Ranch by 2009 because the ranch had by then been intensively managed for livestock for 100+ years; during that time, marmots were shot on sight. In 2009, MPG Ranch was purchased and immediately transitioned into a conservation property. Despite a moratorium on marmot shooting initiated in 2009, the remnant marmot population had not shown signs of recovery by 2013. We therefore began targeted habitat enhancement in 2014 to potentially help restore the marmot population.

We lacked specific information about the reference condition of the marmot population prior to 2009. We therefore made a general prediction that marmots would respond to habitat enhancement by increasing in number and expanding geographically into habitat-enhanced areas. Because social systems of yellow-bellied marmots consist of closely related female kin groups, with mother–daughter–sister groups or matrilines (Armitage 1984, 2002), one benchmark of our restoration work (sensu Block et al. 2001) was that adult females would occupy all enhanced habitat areas. Another benchmark was that adult females in enhanced habitat areas would be reproductively successful. Finally, we evaluated annual survival of the marmot colony and documented sex ratios for comparison with those of other marmot colonies.

MATERIALS AND METHODS

Study area.—Our study was conducted on MPG Ranch (46°42′26″'N, 114°00′16″W), a 6,191-ha conservation property located in the Northern Sapphire Mountains in western Montana, United States (Fig. 1). MPG Ranch consists primarily of open, west-facing, grass-covered slopes with narrow deciduous woody draws that lead to bottomland riparian cover species of the Bitterroot River floodplain (Noson and Rodriguez 2015) with alfalfa fields adjacent to the river. The climate is temperate with sunny summers lasting ~3 months and snowy winters lasting ~5 months. Elevations range from the summit of Mount Baldy (1,833 m) to the river floodplain (966 m). Tree species include Douglas-fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*), Ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*). The marmot colony we studied existed along the western edge of MPG Ranch, adjacent to the Bitterroot River. The entire colony lived in an area of ~2 ha; elevation within the colony area ranged between 1,060 and 1,075 m above sea level.

Habitat enhancement.—Marmots require adequate water, hibernation opportunities, availability of grasses and forbs, and security cover such as rock outcrops (Svendsen 1974; Ozgul et al. 2006), under and near which marmots dig burrows (Blumstein and Pelletier 2005). On MPG Ranch, alfalfa (*Medicago stavia*) and water were available throughout the marmot active period each year, but large rock outcrops were sparse. We therefore focused habitat enhancement efforts on constructing security log piles, which we hoped would serve as surrogates for rock outcrops, where marmots could watch for predators and thermoregulate, as well as dig burrows (hibernacula, natal, and home). We constructed security log piles in the area where the remnant marmot population was observed, near Woodchuck Creek, during 2009–2013 (Original burrows area), and in two additional areas north of the Original burrows area (Middle Cliffs and White Rock burrows areas; Fig. 2). Habitat enhancement efforts spanned 3 years: 2014–2016. During summer 2014, we created one large and two small log piles in the Original burrows area, one large and three small log piles in the Middle Cliffs burrows area, and two small log piles in the White Rock burrows area. During summer 2015, we constructed three small log piles in the Original burrows area and expanded one small log pile in the White Rock burrows area. In summer 2016, we incorporated 49 m² of concrete slabs (each slab was 0.3–1.2 m²) into the large log pile at Middle Cliffs burrows area.

To construct the security log piles, we stacked logs (~20 logs for smaller piles, ~50 logs for larger piles) to a height of ~3 m, like a teepee, covering an area of approximately 2.4 m × 2.4 m for small piles and 4.6 m × 4.6 m for large piles. Logs came from thinning and beetle control actions in the upland forests on MPG Ranch. We used both ponderosa pine brood trees (trees cut while infested with pine bark beetles; 20–50 cm
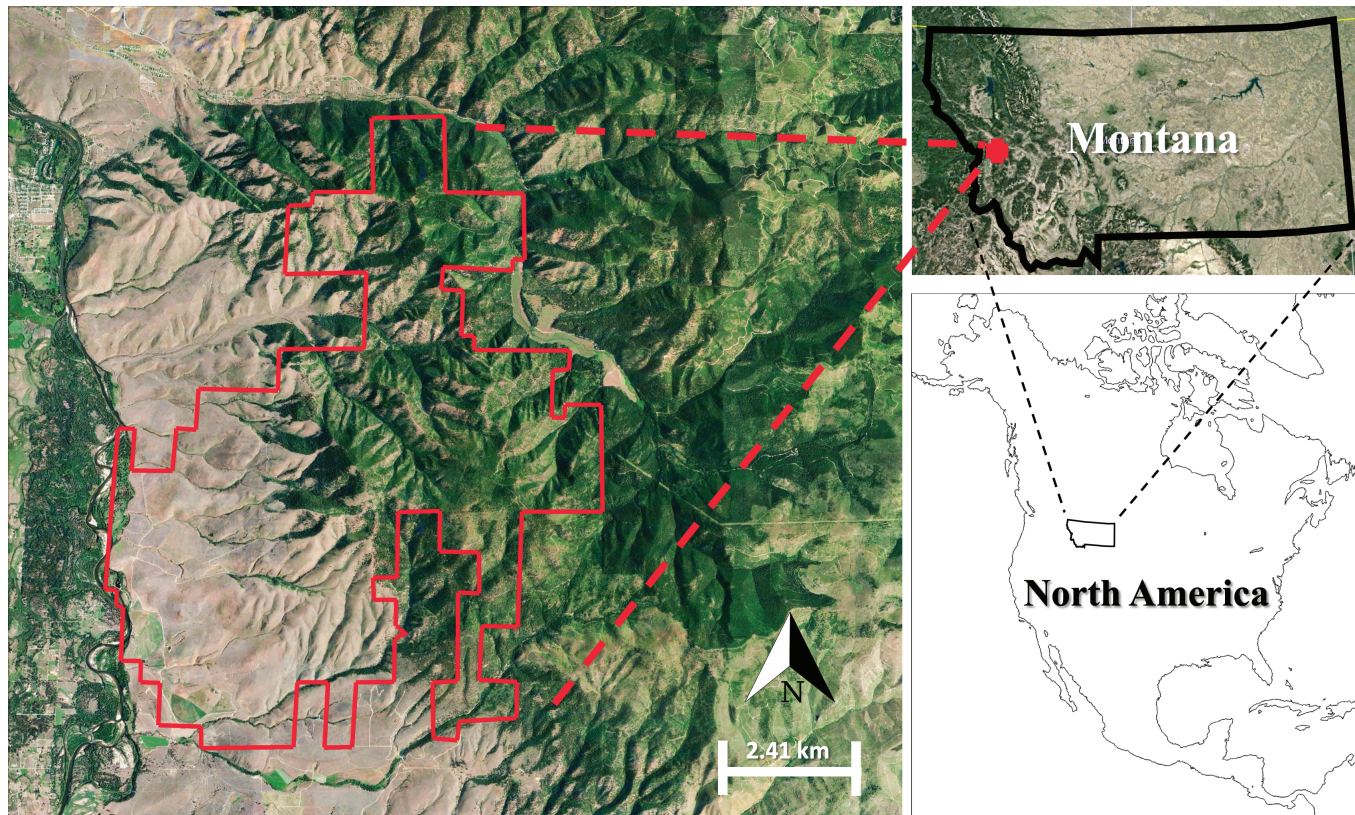
Fig. 1.—The ~2-ha colony of yellow-bellied marmots (*Marmota flaviventris*) was located on the western border of MPG Ranch (red outline), a 6,191-ha conservation property in western Montana.
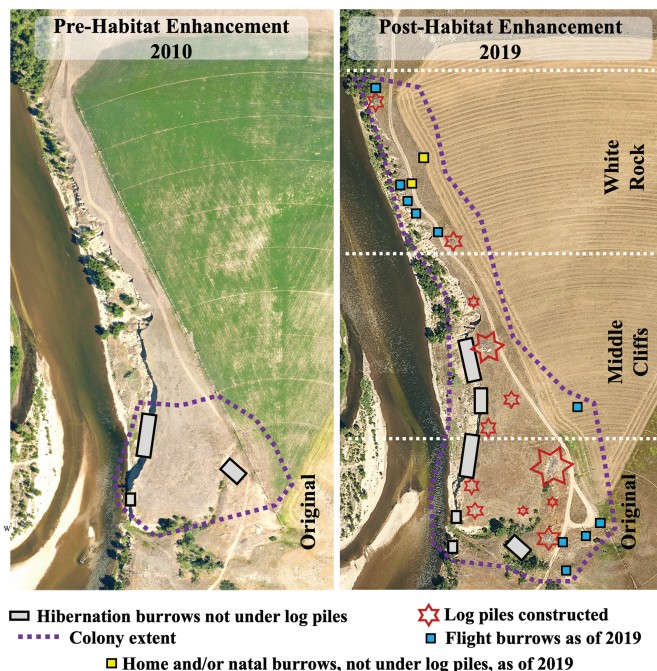

Fig. 2.—The yellow-bellied marmot (*Marmota flaviventris*) colony on MPG Ranch in western Montana, pre- and post-habitat enhancement during 2010–2019. Stars represent areas where we constructed security log piles, gray rectangles represent hibernation burrows constructed by marmots, blue squares represent flight burrows created by marmots, and yellow squares represent home or natal burrows constructed by marmots located near, but not under, security log piles.

stem diameters) and smaller Douglas-fir trees (3–20 cm stem diameters). Log piles were placed near steep banks adjacent to the Bitterroot River and within 200 m of alfalfa fields, which were irrigated throughout each summer season during the study period. Because marmots that disperse > 500 m are less likely to survive (Van Vuren 1990), we placed security log piles < 500 m from other security log piles to minimize mortality due to movements over long distances.

Trapping marmots.—From fall 2013 to spring 2019, we livetrapped yellow-bellied marmots using Tomahawk live trap model 608.5 (Tomahawk Live Trap, Hazelhurst, Wisconsin) for 2 weeks each August, immediately pre-immergence (hereafter termed "fall") and each March or April, immediately post-hibernation and pre-birth (hereafter termed "spring"), except during fall 2015 during which time we trapped only 3 days, and during fall 2017 when trapping was cancelled due to logistical constraints. Except during fall 2015 and fall 2017, we continued trapping until we had reasonable assurance of having captured all marmots on site. We pit tagged each marmot upon first capture (HPT 12PLT 8mm; Biomark, Boise, Idaho), scanned each recaptured marmot (Biomark Global Pocket Reader Plus, Boise, Idaho), recorded trap location, and collected hair for DNA analyses. Beginning in spring 2014, we recorded size based on visual observation (VO; small or large) while marmots were in-hand. If marmots were clearly pups or yearlings, they were documented as "small." If marmots were adults, they were documented as "large." Beginning in fall 2018, we recorded sex while

marmots were in-hand and confirmed sex via DNA analyses. Beginning in spring 2019, we recorded mass (kg). Marmots that weighed < 2 kg were categorized as yearlings and those that weighed ≥ 2 kg were categorized as adults (Borrego et al. 2008). Beginning in early summer 2019, we livetrapped marmot pups immediately post-emergence from natal dens until all pups were thought to have been captured. We weighed, determined the sex, and pit tagged all pups, and we collected hair for DNA analyses to confirm identification and sex. During all trap sessions, we monitored traps from a research station located 1.2 km from the marmot colony, using a network of live-feed video cameras with zoom, tilt, and pan capabilities (Model Q6114-E PTZ Dome; Axis Communications, Lund, Sweden), and processed marmots immediately after capture. Because we used live-feed video to observe marmot captures from a distance, trap effort was intense in that we were able to set and reset traps multiple times daily until we felt all marmots had been captured. In addition to capturing marmots, we observed marmot activity throughout MPG Ranch to identify new sites of marmot occupancy outside the 2-ha colony. We used 243 cameras (75 buckeye cameras with live images, 126 trail cameras, 17 internet protocol cameras, 13 time lapse cameras, and 12 video cameras). All procedures followed ASM guidelines (Sikes et al. 2016) and complied with the requirements of the Institutional Animal Care and Use Committee for Montana Fish Wildlife and Parks (IACUC # FWP16-2013 through IACUC # FWP03-2019, Missoula, Montana).

DNA methods.—We extracted genomic DNA from hair samples using the QIAGEN DnEasy Blood and Tissue kit (Qiagen, Valencia, California) according to the manufacturer's instructions for tissue, and using modifications for hair samples from Mills et al. (2000). We carried out sex identification using DNA by amplifying the male specific minor histocompatibility complex antigen (*Smcy*) along with a microsatellite control using primers *UroSmcF/MarSmcR*, and *GS14F/GS14R* (Gorrell et al. 2012). Reaction volumes of 20 µl contained 50–100 ng DNA, 1× reaction buffer (Thermo Fisher, Carlsbad, California), 2.5 mM MgCl$_2$, 200 µM each dNTP, 1 µM each primer, 1 U Titanium Taq polymerase (Takara Bio USA, Inc., Mountain View, California). The PCR program was 94°C/5 min, [94°C/1 min, 54°C/1 min, 72°C/1 min 30 s] × 34 cycles, 72°C/5 min. The quality and quantity of template DNA were determined by 2.5% agarose gel electrophoresis.

Modeling transition probabilities in a multistate framework.—To evaluate whether the marmot population expanded geographically, we analyzed the capture-reencounter data using a multistate framework to estimate transition probabilities (ψ) among habitat states. We assigned habitat states based on burrow area of marmot capture. Burrow areas were grouped into three categories: Original burrows area, Middle Cliffs burrows area, and White Rock burrows area (Fig. 2). On the rare occasion that a marmot was captured in more than one of the three burrow areas during a single 2-week trapping session, we assigned the first capture location as the habitat state for that marmot for that session.

Encounter histories.—We were interested in evaluating transition probabilities among habitat states throughout the study period, so we created encounter histories based on a 1-season time interval for each marmot during fall 2013 to spring 2019 (i.e., 12 encounter periods). We included fall 2015 and fall 2017 in all marmot encounter histories, but constrained these two encounters to zero. We included data from each fall and spring capture because important information about marmot transitions among habitat states were only obtainable by including both fall and spring data. For example, if marmot x was captured during fall in habitat state "Original burrows area" and recaptured the following spring in habitat state "White Rock burrows area," then evaluating only spring capture data or pooling seasonal data for annual analyses would have resulted in lost information critical to this particular evaluation. Although this data structure was suitable for understanding transition probabilities among habitat states, using seasonal data within a multistate framework to simultaneously estimate annual survival for this population using this data set was not optimal because trap effort was not equal for two fall sessions. We therefore modeled age-structured survival separately using only spring capture data and a Cormack–Jolly–Seber model (see "Modeling age-structured survival" section below).

Modeling transition probabilities.—Data were insufficient to estimate transition probabilities among all three habitat states, so we collapsed the two northernmost burrow areas into one habitat state. Thus, we estimated ψ between the Original burrows area habitat state (O) and the North burrows area habitat state (N), with the latter including Middle Cliffs burrows area and White Rock burrows area. We used the multistate recaptures-only model in Program Mark (White and Burnham 1999) to estimate the probability of individual i transitioning from Original habitat state to North habitat state = $\psi^{ON}_{i,t}$, and the probability of individual i transitioning from North habitat state to Original habitat state = $\psi^{NO}_{i,t}$, between occasion t and $t + 1$, and recapture probability (p). We held survival (φ) constant. We evaluated goodness of fit of the most parameterized model (i.e., the global model) using a bootstrap approach with 1,000 simulations. We estimated the overdispersion parameter (c) and, in the case of overdispersion, we adjusted c-hat accordingly. We used Akaike's information criterion (Akaike 1973) adjusted for sample size (QAIC$_c$) to rank models in terms of their ability to explain the data. Models with ΔQAIC values < 2.0 were considered to have substantial support (Burnham and Anderson 2002). We evaluated Akaike weights for each model.

Prior to modeling transition probabilities between habitat states, we conducted preliminary analyses to determine the best parameterization for recapture probability (p). Based on marmot biology and our study design, p may have been affected by season. Theoretically, p should have been relatively high during spring sessions because spring trapping occurred pre-birth when all marmots in the population would have been available for capture during the previous fall. Similarly, p should have been relatively low during fall sessions because fall trapping occurred post-birth when young of the year were available for first capture. We therefore tested the effect of trap season on p, relative to the fully time-varying model and the null model.

For preliminary analyses, we also wanted to know if *p* was affected by habitat enhancement efforts. We evaluated *p* as a function of three possible pre- and post-habitat enhancement time periods to coincide with the three habitat enhancement periods that occurred at MPG Ranch: 1) habitat enhancement that occurred in summer 2014 {pre-habitat enhancement = time prior to summer 2014}; 2) habitat enhancement that occurred in summer 2015 {pre-habitat enhancement period = time prior to summer 2015}; and 3) habitat enhancement that occurred in summer 2016 {pre-habitat enhancement period = time prior to summer 2016}. For example, we evaluated the effect of restoration efforts that occurred during summer 2014 by constraining *p* among trap sessions prior to summer 2014 (pre-habitat enhancement) to be equal and simultaneously constraining *p* among trap session after summer 2014 (post-habitat enhancement) to be equal.

To account for two missing trap sessions during fall 2015 and fall 2017, we constrained *p* for those two periods to be equal, both of which were zero. We evaluated goodness of fit of the most parameterized model (i.e., the global model) using a bootstrap approach with 1,000 simulations. We estimated c and, in the case of overdispersion, we adjusted c-hat accordingly. We used Akaike's information criterion (Akaike 1973) adjusted for sample size (QAIC$_c$) to rank models in terms of their ability to explain the data. Models with ΔQAIC values < 2.0 were considered to have substantial support (Burnham and Anderson 2002). We evaluated Akaike weights for each model. After selection of the best parameterization for *p*, we modeled habitat transition probabilities ($\psi_{i,t}^{ON}$, $\psi_{i,t}^{NO}$) as a fully time-varying function and as a function of habitat enhancement efforts using the three possible pre- and post-habitat enhancement time periods, using the methods described above for preliminary analyses of *p*.

Modeling age-structured survival.—Using an information theoretic approach (Burnham and Anderson 1998), we evaluated the effect of age structure on apparent survival (the probability that the animal is alive and remains in the study area, hence is available for recapture; φ) and *p*. We created encounter histories, based on a 1-year time interval, for each marmot captured during spring trapping sessions, 2014–2019. We included data only from spring trap sessions to ensure equal trap effort among trap sessions. In so doing, our analyses included annual pre-birth sample data. Pups captured during early summer 2019 were not included in this analysis.

Ideally, it is best to evaluate survival by age class and sex simultaneously, but our sample size of known-sex individuals was too small; we therefore focused on possible age class effect. Marmots that were visually observed as "small" at first capture during spring 2014 to fall 2018, or those that weighed < 2 kg at first capture during spring 2019 were categorized as yearlings at first capture. Marmots that were visually observed as "large" at first capture during spring 2014 to fall 2018, or those that weighed ≥ 2 kg at first capture during spring 2019 were categorized as adults at first capture. During spring 2019 trapping, we conducted a double-blind test to evaluate the accuracy of our early method of categorizing age class based on visual observation of marmot size. For every marmot captured during spring 2019, we first documented age class for each marmot based on VO of marmot size while the marmot was in-hand. We then weighed each marmot and assigned an age class according to mass. We subsequently compared age class based on VO of marmot size, to age class based on marmot mass, for each marmot.

We used an age-structured Cormack–Jolly–Seber model (Lebreton et al. 1992) in Program Mark (White and Burnham 1999) to estimate age specific φ and *p*. Although there can be at least three marmot age classes (juveniles, yearlings, and adults—Ozgul et al. 2006), we included only two age classes (yearlings and adults) because our analyses were based on capture data only collected during spring sessions, when all marmots were either adults or yearlings. Marmots are considered adult by age 2, so we modeled age-structured φ by partitioning φ of yearlings into two groups: 1) φ during the first 1-year interval when yearlings were between 1 and 2 years old; and 2) φ during all other 1-year intervals, after yearlings had transitioned into adults. Survival of marmots categorized as adults at first capture was modeled the same as yearlings that had transitioned to adults.

Apparent survival was bounded between 0 and 1, so we used the logit link to develop models of φ. We modeled φ and *p* as a function of age structure, time, age class (age at first capture without age structure), and the interaction between age class and time. We evaluated goodness of fit of the most parameterized model, φ(*t * g*) *p*(*t * g*), using a bootstrap approach with 1,000 simulations (Franklin et al. 2004). We estimated c and, in the case of overdispersion, we adjusted c-hat accordingly. We used Akaike's information criterion adjusted for sample size (QAIC$_c$—Akaike 1973) to rank models in terms of their ability to explain the data. Models with ΔQAIC values < 2.0 were considered to have substantial support (Burnham and Anderson 2002). We evaluated Akaike weights for each model.

Results

Marmot captures.—During fall and spring trap sessions 2013–2019, we captured 112 individual yearling and adult marmots 319 times. Because we intensively trapped marmots during trap sessions, we believe we captured most individuals of the population that were present and available for capture (or recapture), barring fall 2015 and fall 2017. Overall, the number of unique individuals captured was relatively low at the beginning of the study, increased through spring 2017, decreased during spring 2018, and increased again through spring 2019 (Fig. 3). A relatively small number of marmots were captured pre-habitat enhancement, all of which were localized in the Original burrows area. Post-habitat enhancement, the overall number of marmots captured increased and the number of marmots captured in areas north of the Original burrows area increased. More individuals were captured at the Middle Cliffs burrows area compared to the White Rock burrows area.

We documented sex for 47 unique nonpup individuals (12M:35F) during fall 2018 and spring 2019 (Fig. 4). Most captured marmots in fall 2018 were subadults (95%). By spring
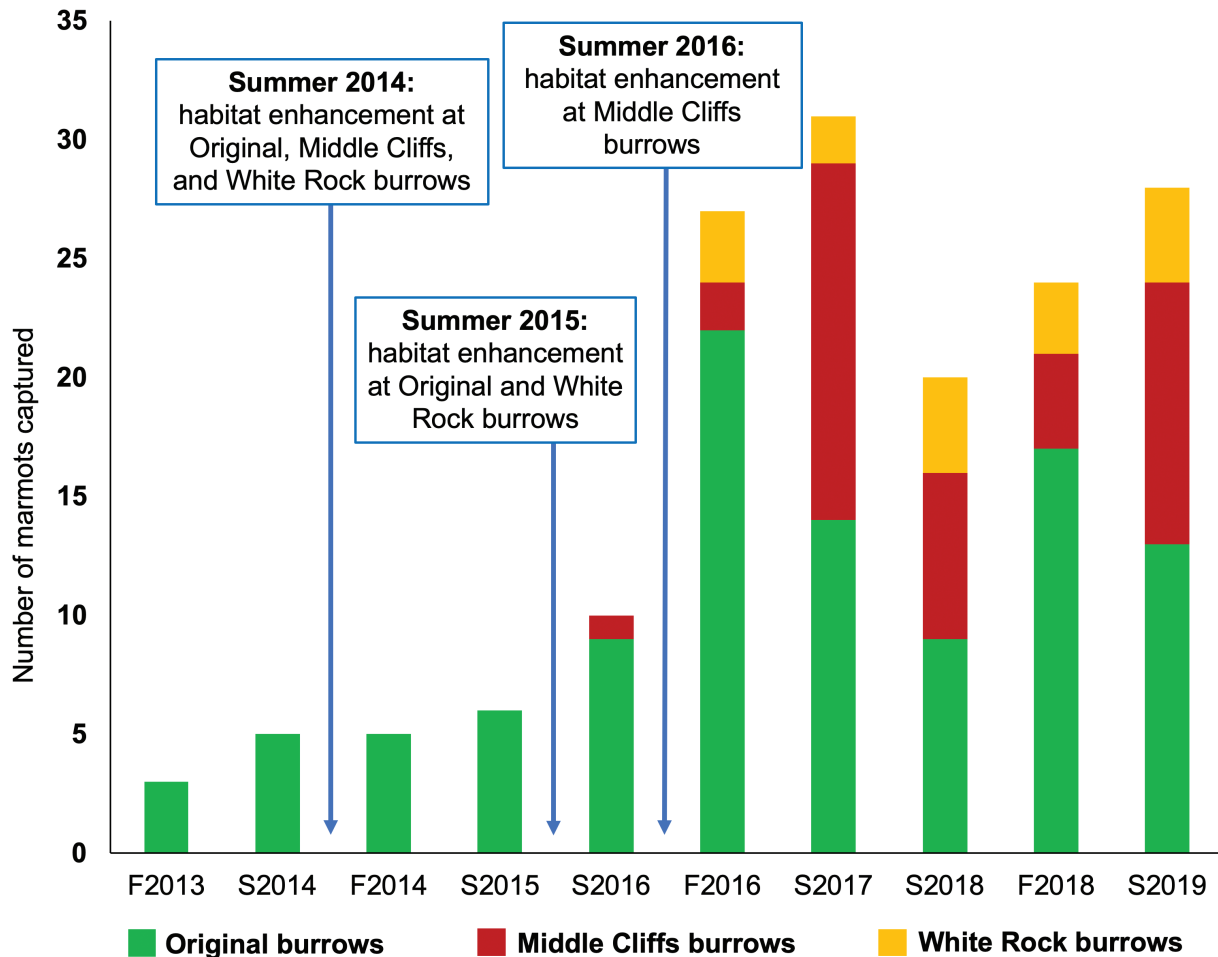
Fig. 3.—The number of unique yellow-bellied marmot (*Marmota flaviventris*) individuals captured at the three burrow areas (Original, Middle Cliffs, and White Rock burrows) during each trap session fall 2013 to spring 2019, in relation to timing of habitat enhancement on MPG Ranch in western Montana. Because research trapping did not occur during fall 2015 or fall 2017, these two trap sessions are not included.

2019, the proportion of subadults captured (57%) was closer to that of adults (43%). All subadults captured during spring 2019 were yearlings, but subadults captured during fall 2018 could not be categorized as juveniles or yearlings because we lacked data on mass for fall 2018. Eleven adult females were captured during spring 2019; six were captured at the Original burrows area, four at Middle Cliffs burrows area, and one at White Rock burrows area. Only one adult female was captured during fall 2018. One adult male was captured during spring 2019; no adult males were captured during fall 2018.

During early summer 2019, we captured 26 marmot pups 144 times. The earliest that pups were observed anywhere on the colony was 24 May, when we began pup trapping. Mean weight of pups was 0.50 kg (95% *CI* = 0.47–0.54). The sex ratio of the young population was 0.44:1 (8M:18F; Fig. 4). Seventeen pups (65%) were captured at the large security log pile in the Middle Cliffs burrows area, two at a small security log pile in the Original burrows area, three at the large security log pile in the Original burrows area, and four at a satellite site next to a burrow on the decommissioned road in the White Rock burrows area.

Based on observations using our large network of video cameras and direct observations by field ecologists who worked during the marmot active period, we documented only seven observations of yearling or adult marmots outside the 2-ha marmot colony during the entire 6-year study period. In spring 2017, two marmots were sighted 2.74 km, and one 1.29 km north, of the 2-ha colony. These three data points could have been three observations of one individual. At the 2.74 km distant location, we successfully captured one adult marmot that was not tagged. It is possible that the untagged adult dispersed from the 2-ha colony and simply had not previously been captured. Alternatively, the individual could have dispersed from the only other known colony nearby, a very small colony located off MPG Ranch about 4.3 km north of the 2-ha colony. In summer 2018, a single marmot was sighted 2.14 km southeast of the 2-ha colony; we do not know from where this marmot dispersed. In summer 2019, a single marmot was observed 635 m east of the 2-ha colony; we successfully trapped the marmot, which was a tagged yearling male. As a result of the foregoing, we had, by 2019, conclusively documented only one male disperser from the 2-ha colony.
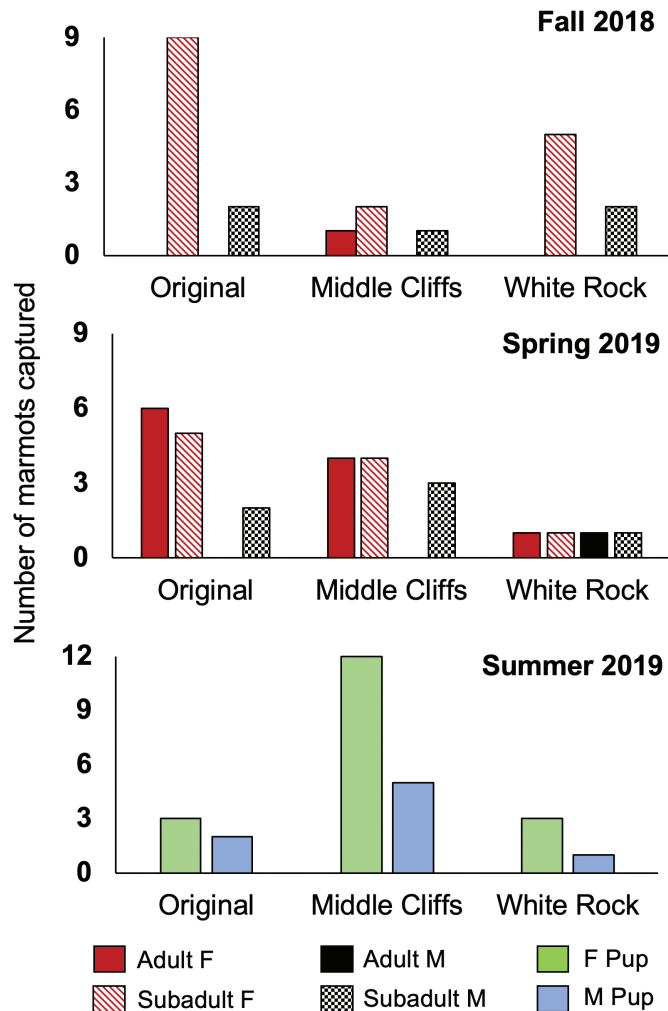
Fig. 4.—Number of yellow-bellied marmots (*Marmota flaviventris*) captured during fall 2018 and spring 2019, by sex and age class, and number of marmot pups captured immediately post-emergence during early summer 2019, by sex, at MPG Ranch in western Montana.

Habitat transition probabilities within a multistate framework—Of the 112 unique yearling and adult marmots we captured, we documented capture location for 109, which as a result was our sample size for habitat transition analyses. C-hat for our preliminary analyses to determine the most parsimonious model for recapture probability (p) was 1.35 so we adjusted for overdispersion. The only model with $\Delta QAIC_c < 2.0$ was $\varphi(.) \, p(\text{season}; \text{F15} = \text{F17}) \, \psi(.)$. As strength of evidence for model selection, the AIC_c weight for the top-ranked model was 0.97, which was at least 33 times more likely to be selected over any other model. The models that included differences in p pre- and post-habitat enhancement ranked very low, as did the null model. All of these low-ranking models had zero weight and zero model likelihood.

Results from preliminary analyses yielded two interesting insights. First, season informed p, which we theorized might occur, given the timing of our field trapping with respect to marmot biology: fall trap sessions occurred post-birth when young of the year were available for first capture (p should have been relatively low), whereas spring trap sessions occurred

pre-birth when all marmots in the population would have been available for capture during the previous fall (p should have been relatively high). That the model of p with season effect was at least 33 times more likely to be selected over any other model underpins the importance of carefully considering possible interactions between species biology and study design, which has implications for other studies. Second, habitat enhancement did not affect p. All three models that included the effects of habitat enhancement on p had zero likelihood, indicating that as the population responded to habitat enhancement by growing in number and expanding geographically, the probability of recapture remained approximately constant.

Using the most parsimonious model of p (season; F15 = F17), we evaluated ψ between Original burrows area and North burrows area, and vice versa. The estimate of c-hat was 1.35 so we adjusted for overdispersion. Four models had $\Delta QAIC_c < 2.0$ (Table 1). The top-ranked model did not include a habitat enhancement effect on transition probabilities, but the other three top-ranking models did. Model weight (ω) for the top-ranked model (0.29) was identical to model weight for the second-ranked model (0.29), indicating strong support for both models. The summed model weights for the three models that included habitat enhancement effect was 0.71.

Based on parameter estimates from the top-ranked model, the probability of transitioning from the Original burrows area to the North burrows area, and vice versa, was 0.17 (0.09, 0.31; Table 2). Based on parameter estimates from the second-ranked model, the probability of transitioning from the Original burrows area to North burrows area pre-habitat enhancement was 0.00 (0.00, 0.00), which differed statistically from the probability of transitioning from the Original burrows area to the North burrows area post-habitat enhancement (0.22; Table 2). The probability of transitioning from the Original burrows area to the North burrows area pre-habitat enhancement also differed statistically from the probability of transitioning from the North burrows area to the Original burrows area at any time during the study.

Age-structured survival.—During spring trapping sessions 2014–2018, we documented marmot size based on VO while marmot was in-hand for 52 individuals (42 S:10 L), and used size to assign age class at first capture for all 52 marmots. In spring 2019, we also began weighing marmots. We weighed 28 individuals and assigned age class at capture according to mass. Of the 28 individuals captured during spring 2019, 20 were recaptured marmots which had previously been assigned age class at first capture. We therefore had information on age class at first capture for a total of 61 individuals (48 yearlings:13 adults). Results of our double-blind test during spring 2019 showed that age class assignment based on VO matched age class assignment based on mass for 26 of the 28 individuals (93% accuracy). The two marmots that were incorrectly assigned age class based on VO weighed close to 2 kg, which was borderline between adult and yearling age classes. In both cases, the marmot size was documented as small (yearling) when, in fact, both marmots weighed slightly more than 2 kg, making them adults.

Table 1.—Model rankings of transition probability (ψ) between the Original burrows area (O) and North burrows area (N), and vice versa, for yellow-bellied marmots (*Marmota flaviventris*) on MPG Ranch in western Montana 2013–2019, where survival (φ) is held constant and recapture rate (p) varies by season, with fall 2015 and fall 2017 constrained to zero. $\Delta QAIC_c$ = difference between model $QAIC_c$ and lowest $QAIC_c$. ω = $QAIC_c$ model weight. k = number of estimable parameters. Deviance = measure of model fit. Model covariates include the three possible habitat pre- and post-habitat enhancement periods (pre- and post-habitat enhancement constructed in 2014, pre- and post-habitat enhancement constructed in 2015, and pre- and post-habitat enhancement constructed in 2016), and the fully time-varying model. Only models with $\Delta QAIC_c$ values < 2.0 are shown, except the null and global models are also shown for comparison.

Model	$\Delta QAIC_c$	ω	Model likelihood	k	Deviance
$\varphi(.)$ p(season; F15 = F17) $\psi(.)$	0.00	0.29	1.00	5	111.13
$\varphi(.)$ p(season; F15 = F17) ψ^{ON}(pre/post 2015[a]) $\psi^{NO}(.)$	0.05	0.29	0.98	7	106.80
$\varphi(.)$ p(season; F15 = F17) ψ^{ON}(pre/post 2014[a]) $\psi^{NO}(.)$	0.53	0.23	0.77	7	107.28
$\varphi(.)$ p(season; F15 = F17) ψ^{ON}(pre/post 2016[a]) $\psi^{NO}(.)$	0.83	0.19	0.66	7	107.58
Null model	42.48	0.00	0.00	6	151.44
Global model	199.43	0.00	0.00	66	72.63

[a] Pre/post YEAR: pre-habitat enhancement = period before summer YEAR, post-habitat enhancement = period after summer YEAR.

Table 2.—Estimates of habitat transition (ψ) probabilities from the top and second-ranked models (from Table 1), with *SE*s and 95% confidence intervals, for yellow-bellied marmots (*Marmota flaviventris*) on the MPG Ranch in western Montana, 2013-2019. * denotes statistical significance. "O" = Original burrow area; "N" = Northern burrows area; pre = prehabitat enhancement; post = post-habitat enhancement.

Model	Parameter	Estimate	SE	Lower confidence interval	Upper confidence interval
$\varphi(.)$ p(season;F15=F17) $\psi(.)$	$\psi(.)$	0.17	0.06	0.09	0.31
$\varphi(.)$ p(season;F15=F17) ψ^{ON} (pre/post 2015) $\psi^{NO}(.)$	ψ^{ON} pre	0.00*	0.00	0.00	0.00
	ψ^{ON} post	0.22	0.06	0.12	0.37
	$\psi^{NO}(.)$	0.06	0.06	0.01	0.40

For analyses of φ, the estimate of c-hat was 1.57 so we adjusted c-hat for overdispersion. Three models had $\Delta QAIC_c$ < 2.0 (Table 3). The top-ranked model was the null model, the second-ranked model included the effect of age structure on φ, and the third-ranked model included the effect of age class (without age structure) on p. As strength of evidence for model selection, the model weight (ω) for the null model was 0.36, compared to 0.20 for the second-ranked model, indicating that the top-ranked model was only 1.8 times more likely to be selected over the second-ranked model. Based on the top-ranked model, φ was 0.63 (0.36, 0.84; Table 4) and p was 0.62 (0.27, 0.87). Based on the second-ranked model, φ for yearlings was 0.50 (0.22, 0.78) and that for adults was 0.71 (0.36, 0.92). Standard error estimates for φ were equal for adults and yearlings (*SE* = 0.16).

DISCUSSION

Our findings showed that the marmot population responded positively to habitat enhancement: the number of marmots captured during trap sessions markedly increased from three marmots pre-habitat enhancement to 54 (28 adults and yearlings, 26 young) post-habitat enhancement by the end of the study, and marmots expanded geographically by transitioning into habitat-enhanced areas post-habitat enhancement. Importantly, adult females occupied and reproduced in all habitat-enhanced areas. Moreover, we observed new flight burrows near the Original burrows area beginning in 2015, and in the Middle Cliffs and White Rock areas beginning in 2016.

Given that our study was observational, we could not rule out the possibility that marmots responded to something other than construction of security log piles. It is possible that the moratorium on marmot shooting alone, which began in 2009, might have been sufficient for the remnant population to recover. However, four years after the shooting moratorium began, only three marmots were captured during an intensive 2-week trap session in fall 2013. On the other hand, the number of marmots captured increased to 31 within only three years of construction of the first security log piles. In addition, the probability that marmots transitioned from the Original burrows area to the Northern burrows area was zero before any security log piles were constructed——the few marmots of the remnant population were localized in the Original burrows area pre-habitat enhancement. After security log piles were constructed, and thus became available to marmots in northern areas, the probability that marmots transitioned to northern areas increased significantly. These findings indicate that active habitat enhancement assisted in the recovery of this degraded system.

Building on previous research focused on using multistate analyses to understand ecological processes, we demonstrated that marmot response to habitat enhancement can be quantified and rigorously analyzed. In particular, to assess whether marmots expanded geographically into enhanced habitat areas, we used a novel approach within a multistate framework. Previous

Table 3.—Model rankings for annual apparent survival (φ) of yellow-bellied marmots (*Marmota flaviventris)* at MPG Ranch in western Montana, 2014–2019. $\Delta QAIC_c$ = difference between model $QAIC_c$ and lowest $QAIC_c$. ω = $QAIC_c$ model weight. k = number of estimable parameters. Deviance = measure of model fit. Model covariates include age structure (yearlings and adults), age class (yearlings and adults), time, and interactions between time and age structure and between time and age class. Only models with $\Delta QAIC_c$ values < 2.0 are shown, except the global model is also shown for comparison.

Model	$\Delta QAIC_c$	ω	Model likelihood	k	Deviance
Null model	0.00	0.36	1.00	2	23.58
φ(age structure) $p(.)$	1.23	0.20	0.54	3	22.59
φ(.) p(age class)	1.94	0.14	0.38	3	23.30
Global model	48.13	0.00	0.00	20	15.38

Table 4.—Estimates of apparent survival (φ) and recapture probability (*p*) from the top and second-ranked models (from Table 3), with *SE*s and 95% *CI*s, for yellow-bellied marmots (*Marmota flaviventris)* on the MPG Ranch in western Montana, 2013–2019.

Model	Parameter	Estimate	*SE*	Lower *CI*	Upper *CI*
Null model	φ	0.63	0.13	0.36	0.84
	p	0.62	0.18	0.27	0.87
φ(age structured) $p(.)$	Yearling φ	0.50	0.16	0.22	0.78
	Adult φ	0.71	0.16	0.36	0.92
	p	0.64	0.17	0.30	0.88

studies have used multistate frameworks to evaluate transition probabilities among age classes (Ozgul et al. 2007; Muths et al. 2014; Prochazka et al. 2017); among habitats (Hotaling et al. 2009; Breininger et al. 2010; Spurgeon et al. 2018); to estimate occupancy (Schmidt et al. 2014; Gorresen et al. 2018; Wilson et al. 2018); and recently to estimate effect of body condition and habitat on survival (Boulanger et al. 2013), and cause-specific mortality (Raithel et al. 2017). Here, we used a multistate framework to estimate the probability (with estimates of error) that a population moved into enhanced habitat areas post-habitat enhancement. This multistate methodology has broad application for wildlife conservation and research aimed at estimating spatial expansion of wildlife populations into restored habitats.

Results from sex ratio analyses yielded surprising insights into this marmot population, as 69% of young captured were female (8M:18F). We were unable to determine sex ratio for every litter based on observation because unlike other marmot colonies where two or more breeding females rarely occupied the same burrow (Armitage 1984), we commonly observed more than three adults and 17 young at one natal log pile. That said, we were able to conclusively determine litter sex ratio for a single female that denned in a discrete satellite site in the White Rock burrows area: the natal den was occupied by only one adult female who shared space with four pups. The litter sex ratio was 1M:3F, consistent with the overall sex ratio of the young population, which was strongly female-biased. Other studies of yellow-bellied marmots found that adult populations were female-biased (Pattie 1967; Armitage 1974) due to differential mortality of dispersing males that are more susceptible to predation (Van Vuren 1990), but none reported strong female bias in young. On the contrary, sex ratio of weaned litters was very close to 1:1 in the Beartooth Mountains of Wyoming (Pattie 1967), the East River Valley in Colorado (Armitage 1974, 1987; Svendsen 1974) and in Yellowstone (Armitage

1962). Our pup trapping methods closely followed that of other marmot studies, particularly in terms of trapping pups within days of emergence and determining sex, and sex of young in our study was confirmed by DNA analyses, so the difference we found in sex ratio of the young population was not likely due to observer error. It may be that female age and recruit status helped explain the female-biased sex ratio of young: younger adult females in Colorado produced female-biased litters compared to older adult females (Armitage 1987) and recruiter females produced more females per litter than did nonrecruiters (Armitage 1984).

Alternatively, the female-biased sex ratio of the young population at MPG Ranch may have been affected by sex ratio adjustment. Under certain circumstances for some populations of polygynous species, "natural selection must favor one or more genes that adjust the sex ratio produced by an adult female to her own condition at the time of parental investment" (Trivers and Willard 1975). In these populations, females in relatively good condition may maximize fitness by investing in male offspring, whereas females in relatively poor condition may maximize fitness by investing in female offspring (Trivers and Willard 1975). For adult female yellow-bellied marmots, the energetically taxing period of parental investment occurs during pregnancy through lactation, the former begins immediately post-emergence in early spring. During this energetically expensive time, prolonged snow cover can negatively affect energy reserves because the hibernation period is extended (Armitage 2013), which can ultimately result in reduced litter size, reproductive frequency, and proportion of female marmots that reproduce (Johns and Armitage 1979; Van Vuren and Armitage 1991; Armitage 2013). Following this line of reasoning, prolonged snow cover resulting in depleted energy reserves would be considered a state of relatively poor condition for adult female marmots.

It is highly likely that marmots on the study site were in relatively poor condition during emergence and mating in 2019 because they experienced an unusually long hibernation period owing to abnormally prolonged snow cover. Snow was still covering over 50% of the colony area (and areas adjacent to the colony area) on 1 April 2019, more than 1 month later than the mean Julian date for 50% snowmelt during the previous 5 years (mean Julian date = 53; 22 February). The first aboveground marmot in 2019 was observed on 25 March, 19 days later than the first aboveground marmot observed in 2018. Because the unusually lengthy period of hibernation in 2019 likely resulted in relatively high depletion of energy reserves, adult females would have been in relatively poor condition during emergence and mating that year, which could have affected sex ratio of offspring according to the Trivers and Willard model. Armitage (1987) previously reported that stress and female age (indicators of body condition) did not affect litter sex ratio of yellow-bellied marmots, and therefore concluded the Trivers and Willard model was not supported. However, the Armitage (1987) study evaluated the effect of social stress and stress chemicals in the blood on litter sex ratio during 2 years, during which time females may not have been subjected to unusually depleted reserves following markedly prolonged snow cover. Given the hypothesis that females will produce the cheaper sex during periods of poor environmental conditions (Myers 1978), additional work to understand proximate causation of sex ratio of yellow-bellied marmot offspring may be warranted.

Survival estimates for adults and yearlings in our study were within the range of those reported for a population of marmots in Colorado that has been studied since 1962. Adult survival in our study was estimated as 0.63 (95% $CI = 0.36$–0.84) and 0.71 (95% $CI = 0.36$–0.92) based on the intercept-only and age-structured models, respectively. Mean adult survival for colonial marmots in Colorado was 0.71 (Oli and Armitage 2004), 0.74 (Ozgul et al. 2007), and 0.76 (Ozgul et al. 2006). Yearling survival in our study was estimated as 0.63 (95% $CI = 0.36$–0.84) and 0.50 (95% $CI = 0.22$–0.78) based on the intercept-only and the age-structured models, respectively, which seemed somewhat higher than survival rates reported for colonial yearlings in Colorado, where mean yearling survival was 0.30 (Ozgul et al. 2006), 0.45 (Ozgul et al. 2007), or ranged from 0.12 to 0.26 (Borrego et al. 2008).

We evaluated apparent survival, which did not account for immigration or emigration. Most yearling male yellow-bellied marmots disperse from their natal area (Armitage 1991), but permanent dispersal appeared relatively low in our study based on observational data. Using a large network of cameras and observations by dozens of field ecologists and landscape restoration staff working throughout the marmot active period, we conclusively documented only one male disperser outside the 2-ha colony site during the entire 6-year study period. It is possible that the minimal observations of dispersing yearlings were due to yearling mortality during dispersal.

Alternatively, it may have been that some yearlings dispersed from their natal dens but remained in the colony. Van Vuren (1990) found that many yearling males dispersed in two stages.

During the first stage, yearlings left natal home ranges and established new home ranges nearby (mean distance = 265 m), then moved further away about 40 days later. Armitage (1991) hypothesized that the first-stage movement likely allowed yearlings to escape social stress from aggressive adult males and the second-stage movement involved locating suitable, unoccupied habitat. If yearlings that were born in the Original burrows area at MPG Ranch dispersed in two stages, they may have established new home ranges in the Middle Cliffs or White Rock areas during the first stage as they sought local refugia from adult males. Because the Middle Cliffs and White Rock areas provided accessibility to food, lookout sites, and hibernacula, yearlings may have forgone the second stage of dispersal and remained at Middle Cliffs or White Rock areas, particularly during the period immediately post-habitat enhancement when these areas should have been unoccupied. Nonetheless, if permanent emigration was higher than what we observed, then our estimates of yearling survival were biased low.

In conclusion, we monitored the response of a remnant marmot population to habitat enhancement in an ecological system that had been dismantled during ~100 years of intensive livestock management, which included eradicating marmots. We found that the marmot population appeared to respond positively to new habitat opportunities created by the construction of security log piles, and gained insights into sex ratio of marmot offspring, which has implications for marmot conservation, ecology, and evolutionary biology. Findings stemming from this work are useful to resource managers interested in restoring degraded landscapes that historically included wild marmots. In addition, the multistate modeling approach we used to evaluate geographic expansion of the marmot population has broad application to other wildlife studies seeking to estimate spatial expansion of populations.

ACKNOWLEDGMENTS

LITERATURE CITED

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in Proceedings of the 2nd International Symposium on Information Theory (B. Petrov and F. Cazakil, eds.). Akadémiai Kiadó. Budapest, Hungary.

ARMITAGE, K. B. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Animal Behavior 10:319–316.

ARMITAGE, K. B. 1974. Male behaviour and territoriality in the yellow-bellied marmot. Journal of Zoology (London) 172:233–265.

ARMITAGE, K. B. 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. Pp. 377–403 in Biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press. Lincoln, Nebraska.

ARMITAGE, K. B. 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring? American Naturalist 129:501–519.

ARMITAGE, K. B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annual Review of Ecology and Systematics 22:379–407.

ARMITAGE, K. B. 2002. Social dynamics of yellow-bellied marmots: strategies for evolutionary success. Pp. 9–21 in Proceedings of the 3rd International Conference on Marmots (K. B. Armitage and Y. Rumiantsev, eds.). ABF Publishing House. Moscow, Russia.

ARMITAGE, K. B. 2013. Climate change and the conservation of marmots. Natural Science 5:36–43.

BLOCK, W. M., A. B. FRANKLIN, J. P. WARD, J. L. GANEY, AND G. C. WHITE. 2001. Design and implementation of monitoring studies to evaluate the success of ecological restoration on wildlife. Restoration Ecology 9:293–303.

BLUMSTEIN, D. T., E. FERNANDO, AND T. STANKOWICH. 2009. A test of the multipredator hypothesis: yellow-bellied marmots respond fearfully to the sight of novel and extinct predators. Animal Behavior 78:873–878.

BLUMSTEIN, D. T., AND D. PELLETIER. 2005. Yellow-bellied marmot hiding time is sensitive to variation in costs. Canadian Journal of Zoology 83:363–367.

BLUMSTEIN, D. T., AND C. RÉCAPET. 2009. The sound of arousal: the addition of novel nonlinearities increases responsiveness in marmot alarm calls. Ethology 115:1074–1081.

BORREGO, N., A. OZGUL, K. B. ARMITAGE, D. T. BLUMSTEIN, AND M. K. OLI. 2008. Spatiotemporal variation in survival of male yellow-bellied marmots. Journal of Mammalogy 89:365–373.

BOULANGER, J., M. CATTET, S. E. NIELSEN, G. STENHOUSE, AND J. CRANSTON. 2013. Use of multi state models to explore relationships between changes in body condition, habitat and survival of grizzly bears (*Ursus arctos horribilis*). Wildlife Biology 19:274–289.

BREININGER, D. R., ET AL. 2010. Multistate modeling of habitat dynamics: factors affecting Florida scrub transition probabilities. Ecology 91:3354–3364.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference; a practical information-theoretic approach. Springer-Verlag Inc. New York.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference. Springer-Verlag Inc. New York.

DAVIDSON, A., ET AL. 2018. Reintroducing a keystone burrowing rodent to restore an arid North American grassland: challenges and successes. Restoration Ecology 26:909–920.

FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIERREZ, AND K. P. BURNHAM. 2004. Population dynamics of the California spotted owl: a meta-analysis. Ornithological Monographs 54:1–555.

GOLET, G. H., T. GARDALI, J. W. HUNT, D. A. KOENIG, AND N. M. WILLIAMS. 2011. Temporal and taxonomic variability in response of fauna to riparian restoration. Restoration Ecology 19:126–135.

GORRELL, J. C., S. BOUTIN, S. RAVEH, P. NEUHAUS, S. D. CÔTÉ, AND D. W. COLTMAN. 2012. Sexing the Sciuridae: a simple and accurate set of molecular methods to determine sex in tree squirrels, ground squirrels and marmots. Molecular Ecology Resources 12:806–809.

GORRESEN, P. M., K. W. BRINCK, M. A. DELISLE, K. MONTOYA-AIONA, C. A. PINZARI, AND F. J. BONACCORSO. 2018. Multi-state occupancy models of foraging habitat use by the Hawaiian hoary bat (*Lasiurus cinereus semotus*). PLoS ONE 13:e0205150.

HARRISON, J. T., M. N. KOCHERT, B. P. PAUL, AND J. A. HEATH. 2019. Using motion-activated trail cameras to study diet and productivity of cliff-nesting golden eagles. Journal of Raptor Research 53:26–37.

HERGET, M. E., K. M. HUFFORD, D. L. MUMMEY, AND L. N. SHREADING. 2015. Consequences of seed origin and biological invasion for early establishment in restoration of a North American grass species. PLoS ONE 10:e0119889.

HOTALING, A., J. MARTIN, AND W. KITCHENS. 2009. Estimating transition probabilities among Everglades wetland communities using multistate models. Wetlands 29:1224–1233.

JOHNS, D. W., AND K. B. ARMITAGE. 1979. Behavioral ecology of alpine yellow-bellied marmots. Behavioral Ecology and Sociobiology 5:133–157.

KENYERES, Z., N. BAUER, L. NAGY, AND S. SZABÓ. 2018. Enhancement of a declining European ground squirrel (*Spermophilus citellus*) population with habitat restoration. Journal for Nature Conservation 45:98–106.

KUMAR, A. V., J. R. SPARKS, AND S. L. MILLS. 2018. Short-term response of snowshoe hares to western larch restoration and seasonal needle drop. Restoration Ecology 26:156–164.

LARSEN, A., J. JACQUOT, P. KEENLANCE, AND H. KEOUGH. 2016. Effects of an ongoing oak savanna restoration on small mammals in Lower Michigan. Forest Ecology and Management 367:120–127.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LEKBERG, Y., S. M. GIBBONS, S. ROSENDAHL, AND P. W. RAMSEY. 2013. Severe plant invasions can increase mycorrhizal fungal abundance and diversity. Multidisciplinary Journal of Microbial Ecology 7:1424–1433.

MALOUF, C. 1974. Economies and land use by the Indians of western Montana. Pp. 117–178 in Interior Salish and Eastern Washington Indians (D. A. Horr, ed.). Garland. New York.

MÉRŐ, T., R. BOCZ, L. POLYAK, G. HORVATH, AND S. LENGYEL. 2015. Local habitat management and landscape-scale restoration influence small-mammal communities in grasslands. Animal Conservation 18:442–450.

MILLER, J. R., AND R. J. HOBBS. 2007. Habitat restoration—do we know what we're doing? Restoration Ecology 15:382–390.

MILLS, L. S., K. L. PILGRIM, M. K. SCHWARTZ, AND K. L. MCKELVEY. 2000. Identifying lynx and other North American felids based on mtDNA. Conservation Genetics 1:285–288.

MULLIGAN, M., R. SCHOOLEY, AND M. WARD. 2013. Effects of connectivity and regional dynamics on restoration of small mammal communities in Midwestern grasslands. Restoration Ecology 21:678–685.

MUMMEY, D. L., AND P. W. RAMSEY. 2017. Can sainfoin improve conditions for establishment of native forbs in crested wheatgrass stands? Ecological Restoration 35:127–137.

MUTHS, E., L. L. BAILEY, AND M. K. WATRY. 2014. Animal reintroductions: an innovative assessment of survival. Biological Conservation 172:200–208.

Myers, J. H. 1978. Sex ratio adjustment under food stress: maximization of quality or numbers of offspring. American Naturalist 112:381–388.

Noson A., and T. Rodriguez. 2015. Relating songbird territories to habitat conditions in woody draw habitats on the MPG Ranch. University of Montana Bird Ecology Lab Annual Report, Missoula, Montana.

Oli, M. K., and K. B. Armitage. 2004. Yellow-bellied marmot population dynamics: demographic mechanisms of growth and decline. Ecology 85:2446–2455.

Ozgul, A., K. B. Armitage, D. T. Blumstein, and M. K. Oli. 2006. Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. Ecology 87:1027–1037.

Ozgul, A., M. K. Oli, L. E. Olson, D. T. Blumstein, and K. B. Armitage. 2007. Spatiotemporal variation in reproductive parameters of yellow-bellied marmots. Oecologia 154:95–106.

Patten, M. 1997. Reestablishment of a rodent community in restored desert scrub. Restoration Ecology 5:156–161.

Pattie, D. L. 1967. Observations on an alpine population of yellow-bellied marmots (*Marmota flaviventris*). Northwest Science 41:96–102.

Prochazka, P., et al. 2017. Delineating large-scale migratory connectivity of reed warblers using integrated multistate models. Diversity and Distributions 23:27–40.

Raithel, J., M. J. Reynolds-Hogland, D. N. Koons, P. Carr, and L. M. Aubry. 2017. Recreational harvest and incident-response protocols reduce human-carnivore conflicts in an anthropogenic landscape. Journal of Applied Ecology 54:1552–1562.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Schmidt, J. H., M. J. Flamme, and J. Walker. 2014. Habitat use and population status of yellow-billed and Pacific loons in western Alaska. The Condor 116:483–492.

SER: Society for Ecological Restoration International Science and Policy Working Group. 2004. The SER international primer on ecological restoration. www.ser.org & Tucson: Society for Ecological Restoration.

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, D. A., and S. D. Gehrt. 2010. Bat response to woodland restoration within urban forest fragments. Restoration Ecology 18:914–923.

Spurgeon, J. J., M. A. Pegg, M. J. Hamel, and K. D. Steffensen. 2018. Spatial structure of large-river fish populations across main-stem and tributary habitats. River Research and Applications 34:807–815.

Stoddard, M., D. Miller, M. Thetford, and L. Branch. 2019. If you build it, will they come? Use of restored dunes by beach mice. Restoration Ecology 27:531–537.

Stokes, E. M., et al. 2011. Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. PLoS ONE 5:e10294.

Suding, K. N. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42:465–487.

Svendsen, G. E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology 55:760–771.

Trivers, R. L., and D. E. Willard. 1975. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Van Vuren, D. 1990. Dispersal of yellow-bellied marmots. Ph.D. dissertation, University of Kansas. Lawrence, Kansas.

Van Vuren, D. 1991. Yellow-bellied marmots as prey of coyotes. American Midland Naturalist 125:135–139.

Van Vuren, D. 2001. Predation on yellow-bellied marmots (*Marmota flaviventis*). American Midland Naturalist 145:94–100.

Van Vuren, D., and K. B. Armitage. 1991. Duration of snow cover and its influence on life history variation in yellow-bellied marmots. Canadian Journal of Zoology 69:1755–1758.

Vesk, P. A., D. Robinson, R. van der Ree, C. M. Wilson, S. Saywell, and M. A. McCarthy. 2015. Demographic effects of habitat restoration for the grey-crowned babbler *Pomatostomus temporalis*, in Victoria, Australia. PLoS ONE 10:e0130153.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Studies 46:120–139.

Wilson, M. C., et al. 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology 31:219–227.

Wilson, T. L., J. H. Schmidt, B. A. Mangipane, R. Kolstrom, and K. K. Bartz. 2018. Nest use dynamics of an undisturbed population of bald eagles. Ecology and Evolution 8:7346–7354.

Wortley, L., J.-M. Hero, and M. Howes. 2013. Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21:537–543.