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DISTRIBUTION, OCCUPANCY, AND HABITAT CORRELATES OF AMERICAN MARTENS (*MARTES AMERICANA*) IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO.

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Summary

1. A clear understanding of marten (*Martes americana*) habitat associations is necessary to effectively manage and monitor populations but was lacking for Rocky Mountain National Park (RMNP).
2. We studied marten distribution and habitat correlates from 2004–2006 in RMNP across 3 spatial scales: 1) site-specific, 2) home-range, and 3) landscape.
3. We used remote-sensored cameras from early August through late October to inventory marten occurrence and modeled occurrence as a function of habitat and landscape variables using binary response (BR) and binomial count (BC) logistic regression, and occupancy modeling (OM). We also assessed which was the most appropriate modeling technique for martens in RMNP.
4. Occupancy modeling appeared to be most appropriate given the explanatory power of derived models and its incorporation of detection probabilities, although the results from BR and BC provided corroborating evidence of important habitat correlates.
5. Occupancy modeling yielded unbiased occupancy values ranging from 91–100% and 20–30% for the western and eastern portions of RMNP, respectively.
6. Location of sites in the western portion of RMNP, riparian mixed conifer stands, and mixed conifer with aspen patches were most frequently positively correlated with marten occurrence, while more xeric and open sites were avoided.

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INTRODUCTION

Many studies have addressed American marten (*Martes americana*; hereafter marten) habitat use (see Buskirk and Powell 1994 and Powell et al. 2003 for reviews), but few included the southern most reaches of marten distribution (Powell et al. 2003) or habitat associations in undisturbed locales. Marten are a species of high interest in Rocky Mountain National Park (RMNP), with preservation of such populations a key management goal of the National Park Service (National Park Service 1988). In RMNP, a combination of highly varied high elevation habitats that straddle the continental divide, and a lack of active forest management provide unique challenges for managing marten populations and habitats. Thus, understanding relationships between martens and available habitats is a key first step toward effectively managing and monitoring marten populations in RMNP.

Traditional approaches to studying wildlife-habitat relationships such as radio-telemetry are frequently expensive and time consuming (MacKenzie et al. 2002; Tyre et al. 2001), especially in remote rugged habitats. Consequently, the use of presence/absence data to quantify these relationships has gained in popularity over the last 15 years (Wintle et al. 2005). Methods such as binary response (BR) or binomial count (BC) logistic regression have most commonly been used to relate species presence to habitat components. However, an occupancy modeling (OM) approach that incorporates imperfect detection into resource selection models has been developed in recent years and provides a viable, less biased alternative (MacKenzie et al. 2005).

Regardless of technique, the spatial scale of analysis is known to result in the selection of different habitat correlates (e.g., Pedlar et al. 1997; Weir and Harestad 2003). For example, in British Columbia, martens appeared to select for stand structure at smaller scales (3.1 ha) but were more frequently associated with climax ecosystems and stand types at larger scales (1,256.6 ha; Mowat 2006). Likewise, martens prefer coarse woody debris and substantial cover at the microsite scale (Buskirk et al. 1989), though such associations are less pronounced at broader scales. Because many habitat attributes are difficult to manage in national parks in part because of a “natural regulation” philosophy, it is important to identify key habitat attributes across multiple spatial scales to provide a suite of potential management options for national park staff. Additionally, little is known about marten habitat use during the summer season. Therefore, as status and critical habitat needs of marten were unknown in RMNP, we assessed marten distribution and use of habitat variables across 3 spatial scales (site-specific, home-range, and landscape scales) using remote-sensored cameras to monitor marten occurrence. Further, we compared results from BR, BC, and OM approaches to relate the different techniques and describe key habitat features for martens in RMNP. Lastly, we derived occupancy values for marten in RMNP. Results should provide needed information on marten habitat use at the southern reaches of its range, as well as identify correlates associated with summer habitat-use patterns of martens.

METHODS

Study area.—Rocky Mountain National Park is a 1,080 km^2 biosphere reserve located in the Rocky Mountain Front Range of northcentral Colorado (Fig. 1). Topography in RMNP was shaped by glaciations, and consists of high mountainous peaks interspersed with small subalpine meadows, lakes, streams, glaciers, and tundra at higher elevations. Elevations range from 2,400–4,345 m. The continental divide bisects RMNP, creating different climatic patterns and vegetation types to the east and west. The eastern part is drier, with precipitation averaging 35.1 cm in the town of Estes Park. Western RMNP is more mesic, with precipitation averaging 50.8 cm in the town of Grand Lake. Seventy-five percent of precipitation falls from April to September. In Estes Park, mean daily high temperatures range from 7.2º C in February to 27.8º C in July, while in Grand Lake, mean daily high temperatures range from 0.0º C in December and January to 23.9º C in July.

Vegetation in RMNP consists of >700 plant species. Community composition varied with more productive communities found on western slopes and at higher elevations (Beidleman et al. 2000). Montane forests and valleys west of the continental divide are comprised primarily of lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) interspersed with bunchgrass and sedge-dominated herbaceous meadows. Montane forests on the eastern slope include the same species though drier sites are often dominated by ponderosa pine (*P. ponderosa*) and Douglas-fir (*Psuedotsuga menziesii*). Subalpine habitats vary less between western and eastern slopes and are dominated by Engelmann spruce (*Picea englemannii*) and subalpine fir (*Abies bifolia*) with limber pine (*Pinus flexilis*) occasionally present. Elevations above timberline (~ 3,500 m) are dominated by tundra and bare rock. Below treeline, wetland and riparian areas are comprised of a variety of species but are dominated by dense stands of spruce-fir and aspen in forested areas (Salas et al. 2005).

A diverse fauna inhabits RMNP including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), Rocky Mountain bighorn sheep (*Ovis canadensis*), black bear (*Ursus americanus*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and coyote (*Canis* *latrans*). Primary food sources for marten in RMNP and surrounding areas include voles (*Microtus* spp.), red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americana*), and a variety of bird and fish species (Gordon 1986).

Camera operation.—We used ArcView 3.3 (Environmental Systems Research Institute, Inc., Redlands, California) to design and plan a saturation trapping grid for camera sites throughout the study area. We placed camera traps at 5-km intervals, which allowed us to cover the entire study area while maximizing sampling effort given financial and temporal constraints. When a pre-selected site was inappropriate (i.e., located on tundra, rocky cliff, etc.), we selected the closest accessible forested site to place the camera.

We used 25 passive infrared-triggered cameras (DeerCam®, Non Typical, Inc., Park Falls, Wisconsin) loaded with 24 exposure 400 ASA film that were programmed to record date and time on photographs. We set time delays on cameras at 2–5 min intervals to maximize repeat photographs while reducing the chance that a single roll of film would be used before it could be replaced. We attached baits consisting of burlap sacks containing sardines and a sweet attractant (usually honey or molasses) to a tree approximately 2 m off the ground and 3–5 m from the camera as an attractant. Because marten sense of smell is fairly limited, the use of bait should not attract individuals from a wide area but rather attract local individuals to the camera site. We checked film, bait, and batteries weekly and removed the camera-sets after 2 weeks for a total of 14 days of operation per site. Occasionally, we left cameras operational for longer durations due to logistical constraints but cameras were operational for a minimum of 14 days in all but 2 cases (10 days for 1 location in 2004; 13 days for 1 location in 2005). Sampling dates were from 10 August–25 October 2004; 12 August–27 October 2005; and 8 August–20 October 2006 with 57 sites sampled each year. We followed guidelines for the care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998) and all activities were in compliance with New Mexico State University Institutional Animal Care and Use Committee Permit 2002–26.

Habitat coverage and data collection.—We related marten occurrence to ≥ 9 habitat variables across 3 scales (site-specific, home-range, and landscape). The use of sampling windows of varying sizes has proven effective in determining habitat use of different species (marten, Mowat 2006; grizzly bear—*Ursus arctos*, Nams et al. 2006) and should provide an appropriate sampling strategy for this investigation. We used the camera location as the sampling point for the site-specific scale. For home-range analyses, we defined a 170-ha sampling window around the camera location and used data collected within this buffer in subsequent analyses. We selected this window size to represent an average home-range size for martens in Colorado (Hoover and Wills 1984). We used a 1,257-ha window to assess habitat correlates at the landscape scale, as a previous study suggested this size was most sensitive to marten detection at the landscape scale (Mowat 2006). We extracted habitat attribute data from GIS coverages of RMNP (Salas et al. 2005) and surrounding areas provided by RMNP staff.

We used forest covertypes (Table 1) and 17 additional habitat variables (Table 2) developed from 30-m resolution raster GIS coverages (Salas et al. 2005) to detect habitat correlates at various spatial scales. Covertype, canopy height, and canopy cover were delineated from 1:12,000-scale, true color aerial photography and ground-truthed for accuracy (Salas et al. 2005). Soil types were georeferenced from Natural Resource Conservation Service soil surveys, and elevation, slope, and aspect were derived from a digital elevation model (Salas et al. 2005).

We selected covertypes and other variables based on potential functional relationships to wildlife use; for example, we included soil types due to known effects on understory productivity and thus potential prey availability (Table 2). We determined correlates at the site-specific scale for the actual location and covertype present at camera sites. Although the extraction of site-specific variables from a GIS could minimize the importance of fine-scale habitat features, (i.e., coarse woody debris), at this scale, more exact measures of fine-scale features are difficult to collect and incorporate into GIS models (Poole et al. 2004). However, most site-specific variables, such as percent canopy cover and other stand or patch structural characteristics, are easily derived from remote imagery and other coarse-scale GIS layers (Davis 2006) and thus accurately modeled at this scale. Variables used for home-range and landscape scales were similar to site-specific factors but calculated separately for their respective sampling windows (Table 2). All covertypes represented the proportion of the window covered by their respective class. Additionally, landscape metrics were calculated for home range and landscape scales using the Patch Analyst extension (Elkie et al. 1999) in ArcView. We selected these metrics based on their depiction of important landscape factors for martens (Potvin et al. 2000).

We also created a 400-m buffer around all human-use areas (trails, roads, and campsites) to assess their impact on marten occurrence at both the home-range and landscape scales (Chapin et al. 1997). The area encompassed within these buffers was removed from each vegetation type and alternatively defined as a human-use covertype. These modified covertypes were compared to unadjusted values to assess what influence human-use areas had on martens.

Last, we included a year effect in analyses to determine if occurrence varied by year, and camera sites were separated into western and eastern subdivisions of RMNP to assess large-scale differences in precipitation and associated vegetative communities caused by orographic lift of air masses between the separate sides.

Data analysis.—We used both BR and BC, which utilizes grouped binary responses in the form of probability values or proportions (Ramsey and Schafer 1997). Although identification of all individuals was impossible, obvious differences in size and coloration indicated multiple individuals visiting many sites, and some sites had multiple individuals included in the same photograph. Therefore, although both techniques were appropriate for our data set, BC was potentially a more powerful approach as it allowed the incorporation of multiple visits to sites. We also used OM to account for imperfect detection of martens at camera sites (MacKenzie et al. 2005). In all cases, we included the measured habitat variables as correlates in models. Additionally, we allocated only 1 visit per day to camera sites for BC and occupancy modeling given our inability to differentiate between individuals.

An implicit assumption of BR and BC approaches is that all individuals present at a sampling location are detected 100% of the time (Gu and Swihart 2004; MacKenzie et al. 2002). Recent studies have shown this is rarely the case (e.g., Kery 2002; Wintle et al. 2005). Deviations from this assumption can result in substantially biased estimates of wildlife-habitat relationships (Gu and Swihart 2004; MacKenzie et al. 2005) and thus result in inappropriate management strategies. However, using an algorithm that incorporates detection probability into the logistic function can account for imperfect detection and results in an unbiased occupancy model (MacKenzie et al. 2005). This OM approach similarly allows the user to incorporate habitat variables in the form of covariates into habitat selection analyses (MacKenzie 2006).

For BC and BR procedures, we divided all length of edge, nearest neighbor, and proximity index measurements by 100 to facilitate interpretation of odds ratios. We conducted logistic regression analyses for each variable individually to assess univariate associations to marten occurrence (PROC LOGISTIC, SAS Institute, Cary, North Carolina). We used

Spearman rank correlations to assess collinearity among variables; if variables were correlated at $r_s \geq 0.70$, only the variable with the lower AIC value was included in further analyses to reduce redundancy (Agresti 1996). Once the data set was reduced, we used the Chi-square score statistic (Hosmer and Lemeshow 2000) to determine the 20 highest scoring models for each level of model parameter size (i.e., 1 through the highest number of parameters in the reduced data set). We compared resultant models using Schwartz information criterion differences (ΔSIC) to determine only those habitat factors most strongly related to occurrence (Link and Barker 2006). Following information criterion protocol, only models with ΔSIC's <4 were considered competing models, with maximum rescaled generalized R^2 values (Nagelkerke 1991) and concordance computed to aid model selection. We used odds ratios to interpret relationships of habitat correlates to marten occurrence.

For OM, we divided covariates with values greater than 10 by an appropriate factor of 10 to keep these values below 10 to facilitate estimation (D. MacKenzie, Proteus Wildlife Research Consultants, pers. comm.). To reduce the variable set and minimize the chance of spurious results, we used only those variables with AIC values less than the null model in further analyses. We assessed correlations between remaining variables as above. Model selection protocol was identical to logistic regression except that concordance values were not calculated. Given the difference in response variables between BR and OM, R^2 values were not comparable. However, they were comparable between OM and those derived for BC. Model 1 (assumes Markovian changes in occupancy) in program PRESENCE (MacKenzie et al. 2003) was used for these analyses. We used odds ratios of variables in the final models to aid interpretation.

We also used OM to calculate adjusted occupancy values that account for imperfect detection of target species (MacKenzie et al. 2005). We determined these occupancy values using the final model selected at each scale for both the western and eastern portions of RMNP. We compared these values to unadjusted occupancy values where unadjusted occupancy = number of sites with marten visits / total number of sites sampled.

RESULTS

We operated camera stations for a total of 2,608 days (850, 868, and 890 days in 2004, 2005, and 2006 respectively), resulting in 140 days (68, 41, and 31 days in 2004, 2005, and 2006 respectively) with marten visits. We photographed martens at 22 of 25 sites on the west side and 6 of 32 sites on the east side with 83.6% of total visits occurring on the western subdivision of RMNP. This resulted in an unadjusted occupancy value of 88.0% and 18.8% for locations on the western and eastern portions of the park, respectively.

Site-specific scale.—Binary response logistic regression indicated that marten detections (Table 3) were most associated with western RMNP (χ^2 = 16.3, P = <0.001; β = 1.746 [SE = 0.432]; odds ratio = 32.9 [95% CI = 6.0–178.7]) but were less likely to be found on eastern aspects (χ^2 = 5.0, P = 0.026; β = –1.208 [SE = 0.542]; odds ratio = 0.09 [95% CI = 0.01–0.75]). The best BC model (Table 3) similarly indicated a preference for the west side of RMNP (χ^2 = 71.4, P = <0.001; β = 1.032 [SE = 0.122]; odds ratio = 7.9 [95% CI = 4.9–12.7]), as well as riparian mixed conifer (χ^2 = 119.1, P = <0.001; β = 1.520 [SE = 0.139]; odds ratio = 20.9 [95% CI = 12.1–36.1]) and sites consisting of hiamovi-rock outcrop soil series (χ^2 = 26.9, P = <0.001; β = 0.659 [SE = 0.127]; odds ratio = 3.7 [95% CI = 2.3–6.1]).

Occupancy modeling (Table 3) also indicated that martens were associated with western localities (χ^2 = 11.8, P = <0.001; β = 3.964 [SE = 1.152]; odds ratio = 52.7 [95% CI = 5.4–512.2]) and riparian mixed conifer (χ^2 = 37.7, P = <0.001; β = 1.528 [SE = 0.249]; odds ratio =

4.6 [95% CI = 2.8–7.5]). This model resulted in an occupancy of 92.9% (SE = 7.0) and 19.8% (SE = 7.3) for the western and eastern subdivisions, respectively.

Home-range scale.—The best BR model (Table 3) found martens were most likely to be located in the western part of the park (χ^2 = 7.9, P = 0.005; β = 5.564 [SE = 1.980]; odds ratio = >999.9 [95% CI = 28.9–>999.9]) in areas with greater amounts of mixed conifer (χ^2 = 4.3, P = 0.038; β = 0.059 [SE = 0.028]; odds ratio = 1.1 [95% CI = 1.0–1.1]) and krummholz edge (χ^2 = 6.0, P = 0.015; β = 0.063 [SE = 0.026]; odds ratio = 1.1 [95% CI = 1.01–1.12]), and with greater distances between shrub riparian cross-zone patches (χ^2 = 4.3, P = 0.039; β = 0.316 [SE = 0.153]; odds ratio = 1.4 [95% CI = 1.0–1.9]). A single observation of martens occurred on the eastern portion of RMNP during 2006 and led to quasi-complete separation of data points, resulting in an unbounded odds ratio for subdivision. Amount of non-vegetated surfaces (χ^2 = 3.5, P = 0.060; β = 4.062 [SE = 2.157]) also appeared in the model, but was uninformative as CI on odds ratios included 1.

The best overall BC model (Table 3) similarly indicated greater occurrence for west side localities (χ^2 = 92.0, P = <0.001; β = 1.141 [SE = 0.119]; odds ratio = 9.8 [95% CI = 6.1–15.6]), specifically those with a larger proportion of riparian mixed conifer stands (χ^2 = 46.3, P = <0.001; β = 0.104 [SE = 0.015]; odds ratio = 1.11 [95% CI = 1.08–1.14]) and a greater number of rock patches (χ^2 = 42.5, P = <0.001; β = 0.099 [SE = 0.015]; odds ratio = 1.10 [95% CI = 1.07–1.14]). Year was also important as higher observation rates occurred the first year (χ^2 = 19.1, P = <0.001; β = 0.419 [SE = 0.094]; odds ratio = 2.3 [95% CI = 1.6–3.3]). An alternative model that included proportion of herbaceous wetland in addition to the previously listed variables yielded similar values (Table 3).

Occupancy modeling (Table 3) also reflected greater occurrence associated with west-side localities (χ^2 = 26.4, *P* = <0.001; β = 24.435 [SE = 4.755]; odds ratio = >999.9 [95% CI = >999.9–>999.9], see above), riparian mixed conifer (χ^2 = 15.1, *P* = <0.001; β = 0.673 [SE = 0.173]; odds ratio = 2.0 [95% CI = 1.4–2.8]), and number of mixed conifer with aspen patches (χ^2 = 5.0, *P* = 0.026; β = 1.205 [SE = 0.540]; odds ratio = 3.3 [95% CI = 1.1–9.7]), though occupancy was negatively related to herbaceous wetlands (χ^2 = 9.5, *P* = 0.002; β = –0.961 [SE = 0.312]; odds ratio = 0.4 [95% CI = 0.2–0.7]). Although present in the model, montane Douglas fir (χ^2 = 2.7, *P* = 0.100; β = –7.336 [SE = 4.509]; odds ratio = 0.001 [95% CI = <0.001–4.8]) was uninformative as CI on odds ratios included 1. Occupancy values for this model were 100.0% (SE = 0.0) for the west side and 28.6% (SE = 11.3) for the east side of RMNP.

Landscape scale.—Binary response logistic regression indicated that west side locations (χ^2 = 6.2, *P* = 0.013; β = 4.235 [SE = 1.700]; odds ratio = >999.9 [95% CI = 6.1–>999.9], see above) in areas with greater amounts of krummholz edge (χ^2 = 3.9, *P* = 0.047; β = 0.020 [SE = 0.010]; odds ratio = 1.02 [95% CI = 1.00–1.04]), larger, less disbursed limber pine stands (χ^2 = 5.4, *P* = 0.021; β = 0.387 [SE = 0.167]; odds ratio = 1.5 [95% CI = 1.1–2.0]), and less interspersion of habitat patches (χ^2 = 5.1, *P* = 0.024; β = –0.737 [SE = 0.327]; odds ratio = 0.5 [95% CI = 0.3–0.9]) were the best indicators of marten occurrence (Table 3). The top BC model (Table 3) indicated greater occurrence in west side localities (χ^2 = 44.0, *P* = <0.001; β = 1.151 [SE = 0.174]; odds ratio = 10.0 [95% CI = 5.1–19.7]) with greater amounts of riparian mixed conifer stands (χ^2 = 21.2, *P* = <0.001; β = 0.181 [SE = 0.039]; odds ratio = 1.2 [95% CI = 1.1–1.3]), more rock edge (χ^2 = 9.6, *P* = 0.002; β = 0.002 [SE = 0.001]; odds ratio = 1.002 [95% CI = 1.001–1.003]), larger, less disbursed rocky areas (χ^2 = 25.1, *P* = <0.001; β = 0.651 [SE = 0.130]; odds ratio = 1.9 [95% CI = 1.5–2.5]), and less edge associated with limber pine stands (χ^2 = 11.4, *P* = <0.001; β = –0.014 [SE = 0.004]; odds ratio = 0.986 [95% CI = 0.978–0.994]). Observations were also recorded more frequently in the first year than subsequent years (χ^2 = 19.8, *P* = <0.001; β = 0.411 [SE = 0.092]; odds ratio = 2.3 [95% CI = 1.6–3.3]).

Occupancy modeling (Table 3) indicated marten occurrence was positively related to west-side localities (χ^2 = 10.1, *P* = 0.001; β = 3.003 [SE = 0.946]; odds ratio = 20.1 [95% CI = 3.1–130.0]) with a greater proportion of riparian mixed conifer sites (χ^2 = 11.4, *P* = <0.001; β = 1.249 [SE = 0.340]; odds ratio = 3.5 [95% CI = 1.7–7.2]), greater interspersion of habitat patches (χ^2 = 13.9, *P* = <0.001; β = 1.034 [SE = 0.277]; odds ratio = 2.8 [95% CI = 1.6–4.9]), and areas with less ponderosa pine edge (χ^2 = 5.8, *P* = 0.016; β = –9.568 [SE = 3.986]; odds ratio = <0.001 [95% CI = <0.001–0.180]) and herbaceous upland edge (χ^2 = 6.8, *P* = 0.009; β = –0.175 [SE = 0.067]; odds ratio = 0.84 [95% CI = 0.74–0.96]). Resultant occupancy rates were 90.0% (SE = 7.0) for the west side and 30.8% (SE = 12.0) for the east side of RMNP.

DISCUSSION

Occupancy probabilities are useful in monitoring and surveying populations but are always underestimated when detection probability is less than 1.0 (Gu and Swihart 2004; MacKenzie et al. 2003). In this study, corrected occupancy estimates varied across scales but were always larger than the unadjusted rates indicating imperfect detection of martens during surveys. The vast majority (>90%) of the western portion of RMNP was occupied by martens while occupancy values were 20–30% for the eastern portion. The association with western localities of RMNP was expressed in all best models regardless of method or scale. Western RMNP was more mesic and had more spruce-fir forest, which is typically preferred over more xeric lodgepole and ponderosa pine stands (Buskirk et al. 1989). This preference was likely related to presence of downed logs and stumps that provided cover and foraging sites (Buskirk et al. 1989; Wilbert et al. 2000), which were more abundant in mesic stands due to less frequent fire occurrence (Thomas et al. 1988).

Commonalities were present among the best supported models at each spatial scale, but the best models were never identical among methods. This variation was not unexpected. For example, BR incorporates only presence or absence at a given site (Ramsey and Schafer 1997), not information regarding the number of days a site was visited or number of individuals that visit a site. Therefore, BC or OM would likely better describe habitat correlates if multiple individuals visited camera sites. Such was the case in our study. Methodological biases therefore likely explain inconsistencies in model selection. For example, at the landscape level, BR models had opposite relationships for mean proximity index of limber pine stands and the interspersion and juxtaposition index when compared to BC and OM.

Further, BC lacks the ability to account for imperfect detection of individuals, and imperfect detection can badly bias habitat models and should be accounted for (Gu and Swihart 2004; MacKenzie 2006; Tyre et al. 2003). Increasing the duration of sampling may help reduce this problem (Gu and Swihart 2004) but will still result in biased estimates unless the detection probability is 1 (MacKenzie et al. 2005). For example, for riparian mixed conifer at both the home-range and landscape scales, odds ratios were greater for OM than for BC, likely because the BC method may be biased due to imperfect detection in our study. Therefore, because of imperfect detection of martens, OM models were likely the most appropriate for RMNP and showed the best fit (R^2) of the selected models.

Despite this, commonalities frequently existed between OM and BC models and corroborated the importance of common variables for martens. Commonalities were mostly related to mesic versus xeric and forested versus open habitat types. For example, riparian mixed conifer stands were strongly related to marten occurrence across all scales (Table 3); this was consistent with other localities where riparian conifer stands served as important foraging (Spencer et al. 1983) and resting (Buskirk et al. 1989) locations. Likewise, patches of mixed conifer with aspen were closely related to riparian mixed conifer stands and likely provided similar foraging and resting opportunities. In contrast, drier forested sites were typically avoided by martens as the presence of ponderosa pine edge precluded occurrence of martens in OM models at the landscape scale, while limber pine edge greatly reduced occurrence in BC models at the same scale.

Martens routinely avoided open habitats (i.e., herbaceous wetlands, and herbaceous uplands) in OM and BC models. Avoidance of open areas has been well documented in other localities (e.g., Hargis et al. 1999; Smith and Schaefer 2002), although one exception appears to be marten use of talus and rock-fields, as these areas provide cover and foraging opportunities for martens (Hoover and Wills 1984; Slauson 2003; Streeter and Braun 1968). While rock variables were selected for by BC models at the home-range and landscape scales, they were not selected in OM models and therefore may be biased. Likewise, of all soil types, only the hiamovi-rock outcrop series was related to marten visits and only in the BC model. This series was characterized by shallow, loamy soils interspersed among rock outcrops (http://www2.ftw.nrcs.usda.gov/osd/dat/H/HIAMOVI.html) and was commonly associated with riparian mixed conifer and mixed conifer with aspen stands (Salas et al. 2005); likely this relationship with preferred covertypes was responsible for its association with marten occurrence. We again caution, however, that these factors were only expressed in BC models and detection probabilities suggest the models may be biased (Gu and Swihart 2004; MacKenzie

2006). Although rocky areas may well have been used by martens in RMNP, they were likely of less importance than mesic forest habitats.

Among landscape metrics, OM indicated that martens were associated only with greater interspersion and juxtaposition values. This preference for a mix of covertypes may reflect their need for multiple habitats throughout the year and their small home ranges (170-ha). For example, although martens avoid open areas during winter, they will occasionally utilize them during summer months (Koehler and Hornocker 1977; Streeter and Braun 1968). Because the landscape scale is meant to reflect a larger habitat utilization pattern, it is not surprising that they selected sites with a greater interspersion of habitats, as several distinct habitat types were associated with marten occurrence in RMNP (Table 3). In contrast, interspersion was not a significant factor in Quebec (Potvin et al. 2000). However, their study was conducted in a clearcut boreal landscape with all coniferous forest types and coniferous plus deciduous forest types pooled into separate categories. This pooling of forest types, along with the presence of active forest management, makes comparisons difficult. Additionally, in contrast to our study, Potvin et al. (2000) assessed marten habitat use during winter. Because marten habitat use and diet composition are known to vary seasonally (Chapin et al. 1997; Cumberland et al. 2001; Gosse and Hearn 2005), it is likely that seasonality could influence the effect of habitat patchiness on marten occurrence. Therefore, interspersion and juxtaposition likely have varying effects on marten occurrence depending on season and forestry practices.

Surprisingly, structural characteristics of stands, such as higher levels of canopy cover and height of stand, that are typically selected for by martens (Buskirk and Powell 1994; Mowat 2006), did not appear in any preferred models. This may be a reflection of the inherent lack of variability in these components in RMNP; little forest management occurred in the park so little variability existed in canopy cover and height values as compared with other forests. Likewise, no models included core-area measurements. Such measurements were found to be important predictors of marten occurrence in other areas (e.g., Maine, Chapin et al. 1998; Quebec, Potvin et al. 2000). However, those sites were extensively logged, likely making such measurements more important in areas of fragmented forest. The fact that RMNP lacks active forest-management practices makes this marten population unique compared to most other populations in North America. It is important to consider the current status of forest structure and fragmentation for a particular area before devising management strategies for martens (Hargis et al. 1999).

Additionally, at home-range and landscape scales, no models indicated that human-use areas affected marten occurrence. Overall, the effect of human-use areas on martens appears to be inconsistent. In northern Ontario, fewer marten tracks were found near roads than farther away from roads (Robitaille and Aubry 2000), whereas investigations in Maine and British Columbia found little impact of human-use areas on marten occurrence (Chapin et al. 1997; Mowat 2006). Our results support these latter findings. Despite significant visitor use (>3 million visitors per year), human impacts are minimal in RMNP as 94% of the park is classified as wilderness (Rocky Mountain National Park Wilderness Act fact sheet 2006). As such, we expected little effect of human density on martens.

Last, it should be noted that most studies have focused on marten use of winter habitat (i.e., Buskirk et al. 1989; Mowat 2006; Wilbert et al. 2000), presumably due to the greater physiological stress associated with the winter season (Hargis and McCullough 1984; Taylor and Buskirk 1994). However, marten habitat use and diet composition varies seasonally (Chapin et al. 1997; Cumberland et al. 2001; Gosse and Hearn 2005). Understanding habitat components beneficial to martens during summer is essential for deriving effective management strategies.

Our results provide further insight into summer habitat use of martens, particularly for southern populations.

CONCLUSIONS

Marten habitat in RMNP during summer was best characterized as mesic west side forests containing abundant riparian mixed conifer stands interspersed with mixed conifer patches containing aspen. In contrast, eastern localities were more xeric with subsequent ponderosa pine and montane Douglas fir stands avoided. Most non-forested sites were avoided (e.g., herbaceous uplands and wetlands) although talus and rock-fields may have been used by martens. Therefore, marten population and habitat management in RMNP should focus on mesic forested sites.

Regardless of the analytical approach, the explanatory value (R^2) of the final models increased from smaller to larger scales, suggesting that broad-scale variables assessed in this study were more important at these larger scales. Mowat (2006) observed a similar trend for comparable scales in British Columbia. His results demonstrated a selection for stand structure at fine scales but climax ecosystems and stand types at the landscape scale. None of the structural variables we assessed were included in the selected models, though resolution of these measurements was coarse. We concur with Poole et al. (2004) that finer detail of site-specific variables (i.e., amount of coarse woody debris) may yield greater insight into resting and foraging preferences of martens for site-specific localities and ultimately stronger results, although such analyses were beyond the scope of this investigation. Therefore, we caution that more emphasis should be placed on models derived at the home-range and landscape scales, though all levels should provide useful information for marten management.

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Table 1. Description of covertypes used to construct marten habitat models for Rocky Mountain National Park, Colorado. Covertypes were derived from vegetation classification maps of RMNP and surrounding areas (Salas et al. 2005).

Covertype	Description
Herbaceous upland	Dry, open meadows
Herbaceous wetland	Herbaceous communities found on wetland or marshy sites
Shrub riparian cross zone	Shrublands lining streambanks and valley bottoms
Shrub upland lower montane	Shrub-dominated communities associated with drier sites
Krummholz	Characterized by stunted limber pine, Engelmann spruce, and subalpine fir at treeline
Dead and down	Characterized by fallen timber from wind, avalanches, or fire
Aspen	Forested site dominated by aspen
Mixed conifer with aspen	Canopy dominated by aspen and mixed conifer species
Riparian mixed conifer	Canopy dominated by spruce/fir species along riparian or seasonally flooded areas
Mixed conifer	Characterized by codominance of two or more coniferous species including Engelmann spruce and subalpine fir
Lodgepole pine	Canopy dominated by lodgepole pine
Limber pine	Canopy dominated by limber pine
Ponderosa pine	Canopy dominated by ponderosa pine
Montane Douglas fir	Canopy dominated by Douglas fir though ponderosa pine can be codominant
Rock	Characterized by rock, bare soil, or snow
Non-vegetated surface	Included areas covered by roads, trails, and campsites

Table 2. List of variables and associated descriptions related to marten occurrence in Rocky Mountain National Park, Colorado. Variables were included into multiple analyses at 3 spatial scales including site-specific (S), home-range (H), and landscape (L) levels with functional relationships (Function) provided for each variable to explain their purpose. Covertypes are described in Table 1.

Variable	Analyses	Description	Function
Covertype	S, H, L	See Table 1	Overstory, understory
Soil type	S	Classification of soil present at camera site	Overstory, understory
Aspect	S	North (316º–45º), east (46º–135º), south (136º–225º), and west categories (226º–315º)	Overstory, understory, climate
Slope	S	Degree slope at camera site	Overstory, understory
Canopy height	S	Height of dominant overstory class coded 1–4: 1 = <1 m, 2 = 1–5 m, 3 = 5–15 m, 4 = 15–30 m	Understory, stand age
Canopy cover	S	Percent closure in canopy coded 1–4: 1 = 75–100, 2 = 50–75, 3 = 25–50, 4 = <25	Understory, stand age
Elevation	S	Elevation above seal level (m) at camera site	Overstory, understory, climate
Core area	H, L	Proportion of sampling window occupied by a core area for each cover type with a 50-m interior buffer	Landscape
Number of patches by covertype	H, L	Number of patches of each covertype present in each sampling window	Landscape
Total number of patches	H, L	Total number of patches summed for all covertypes present in each sampling window	Landscape
Length of edge by covertype	H, L	Length of edge for each covertype present in each sampling window	Landscape
Total length of edge	H, L	Total length of edge summed for all covertypes present in each sampling window	Landscape
Interspersion juxtaposition index	H, L	Measure of patch adjacency	Landscape
Area-weighted mean shape index	H, L	Measure of shape complexity	Landscape
Mean nearest-neighbor index	H, L	Minimum distance to nearest similar patch	Landscape
Mean proximity index	H, L	Measure of degree of isolation and fragmentation; derived using 200-m search radius	Landscape

Table 3. Summary of selected marten habitat-use models at the site-specific (Site), home-range (HR), and landscape (LS) scales for Rocky Mountain National Park. Modeling approaches included binary response logistic regression (BR), binomial count logistic regression (BC), and occupancy modeling (OM). Values reported include likelihood ratio χ^2 statistics (χ^2) and associated *P* values (*P*), Schwartz Information Criterion (SIC) values and the difference in SIC when compared to the top models (ΔSIC), percent concordance (% con), and maximum rescaled generalized R^2 (R^2).

Scale	Method	Model[a]	χ^2	*P*	SIC	ΔSIC	% con	R^2
Site	BR	sub, asp	36.2	<0.001	55.0	0.0	81.8	0.63
	BC	sub, rmc, hm soil	213.2	<0.001	909.6	0.0	69.1	0.23
	OM	sub, rmc	62.9	<0.001	904.6	0.0		0.25
HR	BR	sub, nv, mc_e, k_e, srcz_nn	57.6	<0.001	45.7	0.0	98.2	0.85
	BC	sub, year, rmc, rock_p	188.1	<0.001	942.5	0.0	80.2	0.20
	BC	sub, year, rmc, rock_p, hw	195.3	<0.001	943.1	0.6	80.9	0.21
	OM	sub, rmc, mcwa_p, hw, mdf	76.2	<0.001	914.9	0.0		0.26
LS	BR	sub, k_e, limp_mp, iji	60.8	<0.001	38.4	0.0	98.6	0.87
	BC	sub, year, rmc, rock_e, rock_mp, limp_e	228.3	<0.001	918.1	0.0	83.8	0.25
	OM	sub, rmc, iji, pp_e, hu_e	79.5	<0.001	911.5	0.0		0.27

[a] Variable notation: sub = west vs. east subdivision of RMNP, asp = eastern aspect, rmc = riparian mixed conifer, hm soil = hiamovi-rock outcrop soil series, nv = non-vegetated surface, mc_e = mixed conifer edge, k_e = krummholz edge, srcz_nn = shrub riparian cross-zone nearest neighbor, year = year sampled, rock_p = number of rock patches, hw = herbaceous wetland, mcwa_p = number of mixed conifer with aspen patches, mdf = montane Douglas fir, limp_mp = limber pine mean proximity index, iji = interspersion and juxtaposition index, rock_e = rock edge, rock_mp = rock mean proximity index, limp_e = limber pine edge, pp_e = ponderosa pine edge, and hu_e = herbaceous upland edge.

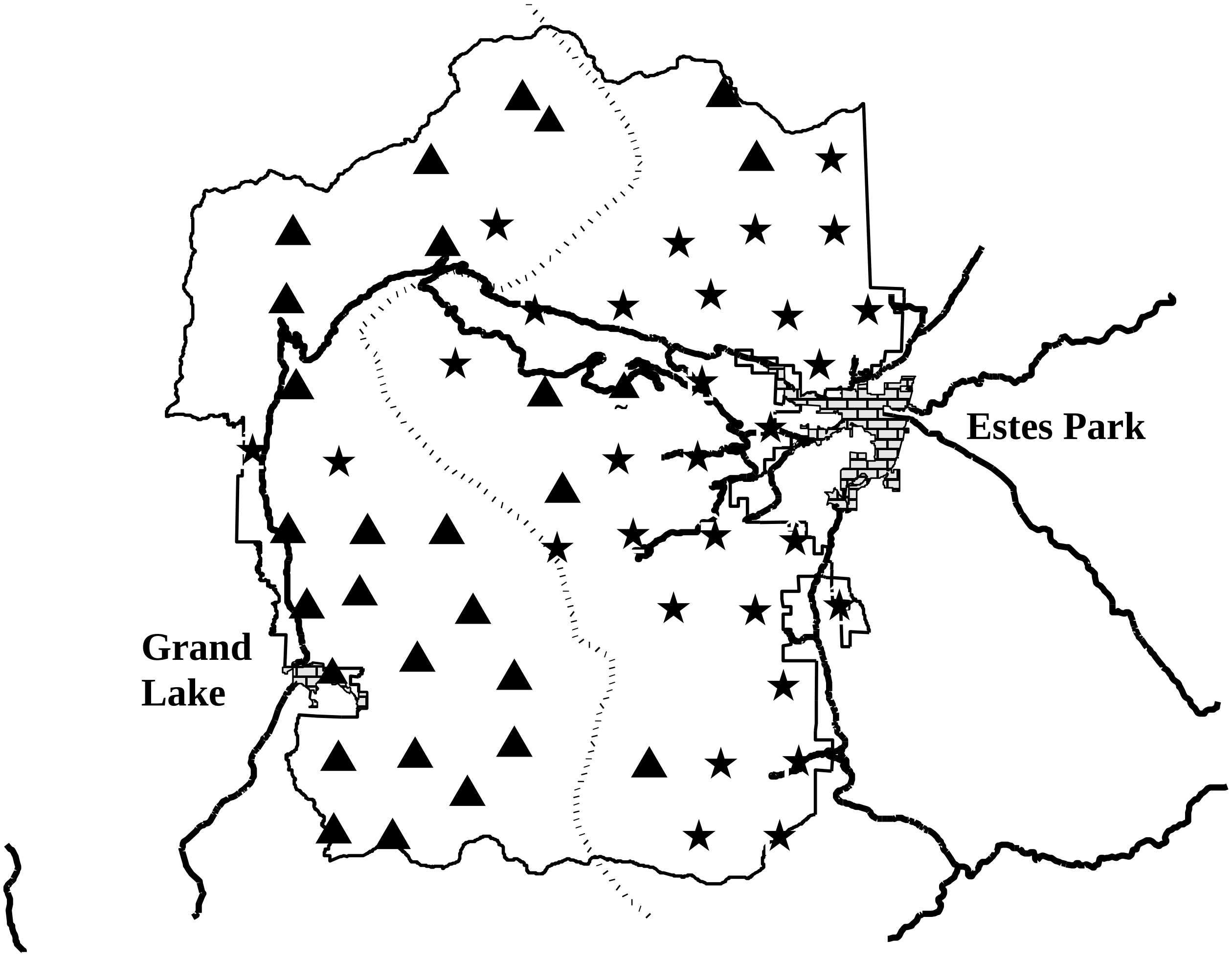

Fig. 1. Map depicting camera locations operated from 2004–2006 to detect marten occurrence in Rocky Mountain National Park, Colorado. Camera locations with marten visits are depicted by ▲, while those without marten visits are marked with ★. The dotted line demarcates the western and eastern subdivisions of RMNP, while the heavy black lines represent park roads and highways.