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

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A clear understanding of habitat associations of martens (*Martes americana*) is necessary to effectively manage and monitor populations. However, this information was lacking for martens in most of their southern range, particularly during the summer season. We studied the distribution and habitat correlates of martens from 2004 to 2006 in Rocky Mountain National Park (RMNP) across 3 spatial scales: site-specific, home-range, and landscape. We used remote-sensored cameras from early August through late October to inventory occurrence of martens 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. Of the 3 modeling techniques, OM 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. Location of sites in the western portion of the park, riparian mixed-conifer stands, and mixed-conifer with aspen patches were most frequently positively correlated with occurrence of martens, whereas more xeric and open sites were avoided. Additionally, OM yielded unbiased occupancy values ranging from 91% to 100% and 20% to 30% for the western and eastern portions of RMNP, respectively.

Key words: detection probability, habitat, logistic regression, marten, *Martes americana*, occupancy, Rocky Mountain National Park

Many studies have addressed habitat use of American martens (*Martes americana*, hereafter martens; see Buskirk and Powell [1994] and Powell et al. [2003] for reviews), but few have included the southernmost reaches of their distribution (Powell et al. 2003) or habitat associations in undisturbed locales. Martens are a species of great 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 populations of martens and their habitats. Thus, understanding relationships between martens and available habitats is a key 1st step toward effectively managing and monitoring populations of martens in RMNP.

Traditional methods for studying wildlife–habitat relationships, such as using radiotelemetry, 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 the presence of a species 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, Canada, 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 preferred coarse woody debris and substantial cover at the

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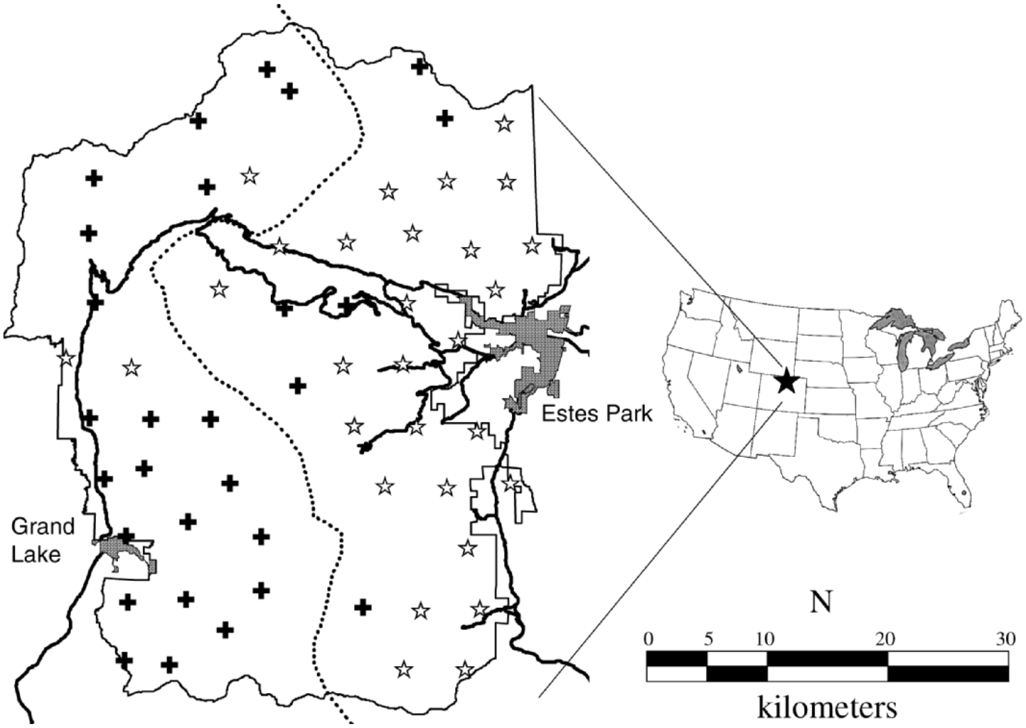

**Fig. 1.**—Map depicting locations of cameras operated from 2004 to 2006 to detect occurrence of martens (*Martes americana*) in Rocky Mountain National Park (RMNP), Colorado. Locations of cameras with visits by martens are depicted by crosses, and those without visits by martens are marked with stars. The dotted line demarcates the western and eastern subdivisions of RMNP, whereas the heavy black lines represent park roads and highways.

microsite scale (Buskirk et al. 1989), although such associations were 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 habitat use by martens during the summer season. Therefore, because status and critical habitat needs of martens were unknown in RMNP, we assessed the distribution of martens and their use of habitat variables across 3 spatial scales (site-specific, home-range, and landscape scales) using remote-sensored cameras to monitor occurrence of martens. 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 martens in RMNP.

## Materials and Methods

*Study area*.—Rocky Mountain National Park is a 1,080-km$^2$ biosphere reserve located in the Rocky Mountain Front Range of north-central 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 to 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 7.2°C in February to 27.8°C in July, whereas in Grand Lake, mean daily high temperatures range from 0.0°C in December and January to 23.9°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, although drier sites are often dominated by ponderosa pine (*P. ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Subalpine habitats vary less between western and eastern slopes and are dominated by Engelmann spruce (*Picea engelmannii*) 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 composed 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 bears (*Ursus americanus*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), and coyotes (*Canis latrans*). Primary food sources for martens in RMNP and surrounding areas include voles (*Microtus*), red squirrels (*Tamiasciurus hudsonicus*), snowshoe hares (*Lepus americanus*), 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 preselected 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- to 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 the sense of smell is fairly limited in martens, 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 because of 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 to 25 October 2004, 12 August to 27 October 2005, and 8 August to 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 (Gannon et al. 2007) 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 occurrence of martens to $\geq 9$ 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 (martens—Mowat 2006; grizzly bears [*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, because a previous study suggested this size was most sensitive to detection of martens at the landscape scale (Mowat 2006). We extracted data on habitat attributes from geographic information system coverages of RMNP (Salas et al. 2005) and surrounding areas provided by RMNP staff.

TABLE 1.—Description of cover types used to construct habitat models for martens (*Martes americana*) for Rocky Mountain National Park (RMNP), Colorado. Cover types were derived from vegetation classification maps of RMNP and surrounding areas (Salas et al. 2005).

| Cover type | 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 2 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 although ponderosa pine can be codominant |
| Rock | Characterized by rock, bare soil, or snow |
| Nonvegetated surface | Included areas covered by roads, trails, and campsites |

We used forest cover types (Table 1) and 17 additional habitat variables (Table 2) developed from 30-m-resolution raster geographic information system coverages (Salas et al. 2005) to detect habitat correlates at various spatial scales. Cover type, 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 cover types and other variables based on potential functional relationships to use by wildlife; for example, we included soil types because of 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 cover type present at camera sites. Although the extraction of site-specific variables from a geographic information system 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 geographic information system models (Poole et al. 2004). However, most site-specific variables, such as percent canopy cover and other structural

**TABLE 2.**—List of variables and associated descriptions related to occurrence of martens (*Martes americana*) 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. Cover types are described in Table 1.

| Variable | Analyses | Description | Function |
|---|---|---|---|
| Cover type | S, H, L | See Table 1 | Overstory, understory |
| Soil type | S | Classification of soil present at camera site | Overstory, understory |
| Aspect | S | North (316°–45°), east (46°–135°), south (136°–225°), and west (226°–315°) categories | 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 sea 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 cover type | H, L | Number of patches of each cover type present in each sampling window | Landscape |
| Total number of patches | H, L | Total number of patches summed for all cover types present in each sampling window | Landscape |
| Length of edge by cover type | H, L | Length of edge for each cover type present in each sampling window | Landscape |
| Total length of edge | H, L | Total length of edge summed for all cover types 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 |

characteristics of stands or patches, are easily derived from remote imagery and other coarse-scale geographic information system 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 cover types 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 cover type. These modified cover types were compared to unadjusted values to assess what influence human-use areas had on martens.

Finally, 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 of RMNP.

*Data analysis.*—We used both BR and BC, which use 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 because 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 OM 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 that 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 measurements of length of edge, nearest neighbor, and the proximity index by 100 to facilitate interpretation of odds ratios. We conducted

**Table 3.**—Summary of selected models for habitat use by martens (*Martes americana*) at the site-specific (Site), home-range (HR), and landscape (LS) scales for Rocky Mountain National Park (RMNP), Colorado. Modeling approaches included binary response logistic regression (BR), binomial count logistic regression (BC), and occupancy modeling (OM). Values reported include likelihood ratio chi-square statistics ($\chi^2$) and associated *P*-values (*P*), Schwartz information criterion (SIC) values and the difference in SIC when compared to the top models ($\Delta$SIC), percent concordance (% con), and maximum rescaled generalized $R^2$ ($R^2$).

| Scale | Method | Model[a] | $\chi^2$ | *P* | SIC | $\Delta$SIC | % 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 versus east subdivision of RMNP, asp = eastern aspect, rmc = riparian mixed conifer, hm_soil = hiamovi-rock outcrop soil series, nv = nonvegetated 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.

logistic regression analyses for each variable individually to assess univariate associations to occurrence of martens (PROC LOGISTIC; SAS Institute Inc., 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 Akaike information criterion (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 ($\Delta$SIC) to determine only those habitat factors most strongly related to occurrence (Link and Barker 2006). Following information criterion protocol, only models with $\Delta$SICs $< 4$ 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 occurrence of martens.

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 visits by martens. 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 detections of martens (Table 3) were most associated with western RMNP ($\chi^2 = 16.3$, $P < 0.001$; $\beta = 1.746$ [$SE = 0.432$]; odds ratio = 32.9 [95% confidence interval (95% *CI*) = 6.0–178.7]) but were less likely to be found on eastern aspects ($\chi^2 = 5.0$, $P = 0.026$; $\beta = -1.208$ [$SE = 0.542$]; 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 ($\chi^2 = 71.4$, $P < 0.001$; $\beta = 1.032$ [$SE = 0.122$]; odds ratio = 7.9 [95% *CI* = 4.9–12.7]), as well as riparian mixed conifer ($\chi^2 = 119.1$, $P < 0.001$; $\beta = 1.520$ [$SE = 0.139$]; odds ratio = 20.9 [95% *CI* = 12.1–36.1]) and sites consisting of hiamovi-rock outcrop soil series ($\chi^2 = 26.9$, $P < 0.001$; $\beta = 0.659$ [$SE = 0.127$]; odds ratio = 3.7 [95% *CI* = 2.3–6.1]).

Occupancy modeling (Table 3) also indicated that martens were associated with western localities ($\chi^2 = 11.8$, $P < 0.001$; $\beta = 3.964$ [$SE = 1.152$]; odds ratio = 52.7 [95% *CI* = 5.4–512.2]) and riparian mixed conifer ($\chi^2 = 37.7$, $P < 0.001$; $\beta = 1.528$ [$SE = 0.249$]; 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 that martens were most likely to be located in the western part of the park ($\chi^2 = 7.9$, $P = 0.005$; $\beta = 5.564$ [*SE* = 1.980]; odds ratio = >999.9 [95% *CI* = 28.9–>999.9]) in areas with greater amounts of mixed conifer ($\chi^2 = 4.3$, $P = 0.038$; $\beta = 0.059$ [*SE* = 0.028]; odds ratio = 1.1 [95% *CI* = 1.0–1.1]) and krummholz edge ($\chi^2 = 6.0$, $P = 0.015$; $\beta = 0.063$ [*SE* = 0.026]; odds ratio = 1.1 [95% *CI* = 1.01–1.12]), and with greater distances between shrub riparian cross-zone patches ($\chi^2 = 4.3$, $P = 0.039$; $\beta = 0.316$ [*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 nonvegetated surfaces ($\chi^2 = 3.5$, $P = 0.060$; $\beta = 4.062$ [*SE* = 2.157]) also appeared in the model, but was uninformative as because *CI*s on odds ratios included 1.

The best overall BC model (Table 3) similarly indicated greater occurrence for west-side localities ($\chi^2 = 92.0$, $P < 0.001$; $\beta = 1.141$ [*SE* = 0.119]; odds ratio = 9.8 [95% *CI* = 6.1–15.6]), specifically those with a larger proportion of riparian mixed-conifer stands ($\chi^2 = 46.3$, $P < 0.001$; $\beta = 0.104$ [*SE* = 0.015]; odds ratio = 1.11 [95% *CI* = 1.08–1.14]) and a greater number of rock patches ($\chi^2 = 42.5$, $P < 0.001$; $\beta = 0.099$ [*SE* = 0.015]; odds ratio = 1.10 [95% *CI* = 1.07–1.14]). Year also was important because higher observation rates occurred during the 1st year ($\chi^2 = 19.1$, $P < 0.001$; $\beta = 0.419$ [*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 ($\chi^2 = 26.4$, $P < 0.001$; $\beta = 24.435$ [*SE* = 4.755]; odds ratio = >999.9 [95% *CI* = >999.9–>999.9], see above), riparian mixed conifer ($\chi^2 = 15.1$, $P < 0.001$; $\beta = 0.673$ [*SE* = 0.173]; odds ratio = 2.0 [95% *CI* = 1.4–2.8]), and number of mixed-conifer with aspen patches ($\chi^2 = 5.0$, $P = 0.026$; $\beta = 1.205$ [*SE* = 0.540]; odds ratio = 3.3 [95% *CI* = 1.1–9.7]), although occupancy was negatively related to herbaceous wetlands ($\chi^2 = 9.5$, $P = 0.002$; $\beta = -0.961$ [*SE* = 0.312]; odds ratio = 0.4 [95% *CI* = 0.2–0.7]). Although present in the model, montane Douglas-fir ($\chi^2 = 2.7$, $P = 0.100$; $\beta = -7.336$ [*SE* = 4.509]; odds ratio = 0.001 [95% *CI* = <0.001–4.8]) was uninformative because *CI*s 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 ($\chi^2 = 6.2$, $P = 0.013$; $\beta = 4.235$ [*SE* = 1.700]; odds ratio = >999.9 [95% *CI* = 6.1–>999.9], see above) in areas with greater amounts of krummholz edge ($\chi^2 = 3.9$, $P = 0.047$; $\beta = 0.020$ [*SE* = 0.010]; odds ratio = 1.02 [95% *CI* = 1.00–1.04]), larger, less-disbursed limber pine stands ($\chi^2 = 5.4$, $P = 0.021$; $\beta = 0.387$ [*SE* = 0.167]; odds ratio = 1.5 [95% *CI* = 1.1–2.0]), and less interspersion of habitat patches ($\chi^2 = 5.1$, $P = 0.024$; $\beta = -0.737$ [*SE* = 0.327]; odds ratio = 0.5 [95% *CI* = 0.3–0.9]) were the best indicators of the occurrence of martens (Table 3). The top BC model (Table 3) indicated greater occurrence in west-side localities ($\chi^2 = 44.0$, $P < 0.001$; $\beta = 1.151$ [*SE* = 0.174]; odds ratio = 10.0 [95% *CI* = 5.1–19.7]) with greater amounts of riparian mixed-conifer stands ($\chi^2 = 21.2$, $P < 0.001$; $\beta = 0.181$ [*SE* = 0.039]; odds ratio = 1.2 [95% *CI* = 1.1–1.3]), more rock edge ($\chi^2 = 9.6$, $P = 0.002$; $\beta = 0.002$ [*SE* = 0.001]; odds ratio = 1.002 [95% *CI* = 1.001–1.003]), larger, less disbursed rocky areas ($\chi^2 = 25.1$, $P < 0.001$; $\beta = 0.651$ [*SE* = 0.130]; odds ratio = 1.9 [95% *CI* = 1.5–2.5]), and less edge associated with limber pine stands ($\chi^2 = 11.4$, $P < 0.001$; $\beta = -0.014$ [*SE* = 0.004]; odds ratio = 0.986 [95% *CI* = 0.978–0.994]). Observations were also recorded more frequently in the 1st year than subsequent years ($\chi^2 = 19.8$, $P < 0.001$; $\beta = 0.411$ [*SE* = 0.092]; odds ratio = 2.3 [95% *CI* = 1.6–3.3]).

Occupancy modeling (Table 3) indicated that occurrence of martens was positively related to west-side localities ($\chi^2 = 10.1$, $P = 0.001$; $\beta = 3.003$ [*SE* = 0.946]; odds ratio = 20.1 [95% *CI* = 3.1–130.0]) with a greater proportion of riparian mixed-conifer sites ($\chi^2 = 11.4$, $P < 0.001$; $\beta = 1.249$ [*SE* = 0.340]; odds ratio = 3.5 [95% *CI* = 1.7–7.2]), greater interspersion of habitat patches ($\chi^2 = 13.9$, $P < 0.001$; $\beta = 1.034$ [*SE* = 0.277]; odds ratio = 2.8 [95% *CI* = 1.6–4.9]), and areas with less ponderosa pine edge ($\chi^2 = 5.8$, $P = 0.016$; $\beta = -9.568$ [*SE* = 3.986]; odds ratio = <0.001 [95% *CI* = <0.001–0.180]) and herbaceous upland edge ($\chi^2 = 6.8$, $P = 0.009$; $\beta = -0.175$ [*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 <1.0 (Gu and Swihart 2004; MacKenzie et al. 2003). In our 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, whereas 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 by martens 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 because of less frequent occurrence of fire (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 the 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 occurrence of martens across all scales (Table 3); this was consistent with other localities where riparian conifer stands served as important locations for foraging (Spencer et al. 1983) and resting (Buskirk et al. 1989). Likewise, patches of mixed conifer with aspen were closely related to riparian mixed-conifer stands and likely provided similar opportunities for foraging and resting. In contrast, drier forested sites were typically avoided by martens, because the presence of ponderosa pine edge precluded occurrence of martens in OM models at the landscape scale, whereas limber pine edge greatly reduced occurrence of martens 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 1 exception appears to be use of talus and rock fields by martens, because these areas provide cover and foraging opportunities for martens (Hoover and Wills 1984; Slauson 2003; Streeter and Braun 1968). Although 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 visits by martens 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 cover types was responsible for its association with occurrence of martens. However, we again caution that these factors were only expressed in BC models and detection probabilities suggest that 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 cover types 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 use them during summer months (Koehler and Hornocker 1977; Streeter and Braun 1968). Because the landscape scale is meant to reflect a larger-scale pattern of habitat use, it is not surprising that they selected sites with a greater interspersion of habitats, because several distinct habitat types were associated with occurrence of martens in RMNP (Table 3). In contrast, interspersion was not a significant factor in Quebec, Canada (Potvin et al. 2000). However, that study was conducted in a clear-cut 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 habitat use by martens during winter. Because habitat use and diet composition of martens 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 occurrence of martens. Therefore, interspersion and juxtaposition likely have varying effects on occurrence of martens 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 measurements of core areas. Such measurements were found to be important predictors of occurrence of martens 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 population of martens 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 occurrence of martens. Overall, the effect of human-use areas on martens appears to be inconsistent. In northern Ontario, Canada, 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 occurrence of martens (Chapin et al. 1997; Mowat 2006). Our results support these latter findings. Despite considerable use by visitors (>3 million visitors per year), human impacts are minimal in RMNP because 94% of the park is classified as wilderness (Rocky Mountain National Park Wilderness Act fact sheet 2006; http://www.wilderness.org/Library/Documents/upload/Factsheet-RockyMtnNationalParkWildernessAct.pdf). As such, we expected little effect of human density on martens.

Regardless of the analytical approach, the explanatory value ($R^2$) of the final models increased from smaller to larger scales, suggesting that broadscale 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, although 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 our investigation. Therefore, we caution that more emphasis should be placed on models derived at the home-range and landscape scales, although all levels should provide useful information for marten management.

Finally, most studies have focused on use of winter habitat by martens (i.e., Buskirk et al. 1989; Mowat 2006; Wilbert et al. 2000), presumably because of the greater physiological stress associated with the winter season (Hargis and McCullough 1984; Taylor and Buskirk 1994). However, habitat use and diet composition of martens vary 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 habitat use of martens in summer, particularly for southern populations.

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## LITERATURE CITED

Agresti, A. 1996. An introduction to categorical data analysis. John Wiley & Sons, Inc., New York.

Beidleman, L. H., R. G. Beidleman, and B. E. Willard. 2000. Plants of Rocky Mountain National Park. Falcon Publishing, Inc., Helena, Montana.

Buskirk, S. W., S. C. Forrest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting site ecology of marten in the central Rocky Mountains. Journal of Wildlife Management 53:191–196.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pp. 283–296 in Martens, sables and fishers: biology and conservation (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.

Chapin, T. G., D. J. Harrison, and D. D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. Conservation Biology 12:1327–1337.

Chapin, T. G., D. J. Harrison, and D. M. Phillips. 1997. Seasonal habitat selection by marten in an untrapped forest preserve. Journal of Wildlife Management 61:707–717.

Cumberland, R. E., J. A. Dempsey, and G. J. Forbes. 2001. Should diet be based on biomass? Importance of larger prey to the American marten. Wildlife Society Bulletin 29:1125–1130.

Davis, R. W. 2006. A GIS-based habitat model predicting elk nutritional condition in the Pacific Northwest. Ph.D. dissertation, University of Illinois, Urbana.

Elkie, P. C., R. S. Rempel, and A. P. Carr. 1999. Patch Analyst user's manual. Ontario Ministry of Natural Resources, Thunder Bay, Northwest Science and Technology, Technical Manual TM-002:1–22.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Gordon, C. C. 1986. Winter food habits of the pine marten in Colorado. Great Basin Naturalist 46:166–168.

Gosse, J. W., and G. J. Hearn. 2005. Seasonal diets of Newfoundland martens, *Martes americana atrata*. Canadian Field-Naturalist 119:43–47.

Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biological Conservation 116:195–203.

Hargis, C. D., J. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. Journal of Applied Ecology 36:157–172.

Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. Journal of Wildlife Management 48:140–146.

Hoover, R. L., and D. L. Wills. 1984. Managing forested lands for wildlife. Colorado Division of Wildlife in cooperation with United States Department of Agriculture Forest Service, Rocky Mountain Region, Denver, Colorado.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. 2nd ed. John Wiley & Sons, Inc., New York.

Kery, M. 2002. Inferring the absence of a species: a case study of snakes. Journal of Wildlife Management 66:330–338.

Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. Journal of Wildlife Management 41:500–505.

Link, W. A., and R. J. Barker. 2006. Model weights and the foundations of multimodel inference. Ecology 87:2626–2635.

MacKenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. Journal of Wildlife Management 70:367–374.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2005. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California.

Mowat, G. 2006. Winter habitat associations of American martens *Martes americana* in interior wet-belt forests. Wildlife Biology 12:51–61.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Nams, V. O., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes—an example with grizzly bears. Biological Conservation 128:109–119.

National Park Service. 1988. Management policies. United States Department of the Interior, Washington, D.C.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. Journal of Wildlife Management 61:102–112.

Poole, K. G., A. D. Porter, A. De Vries, C. Maundrell, S. D. Grindal, and C. Cassady St. Clair. 2004. Suitability of a young deciduous-dominated forest for American marten and the effects of forest removal. Canadian Journal of Zoology 82:423–435.

Potvin, F., L. Bélanger, and K. Lowell. 2000. Marten habitat selection in a clearcut boreal landscape. Conservation Biology 14:844–857.

Powell, R. A., S. W. Buskirk, and W. J. Zielinski. 2003. Fisher and marten. Pp. 635–649 in Wild mammals of North America (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). Johns Hopkins University Press, Baltimore, Maryland.

Ramsey, F. L., and D. W. Schafer. 1997. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, California.

Robitaille, J.-F., and K. Aubry. 2000. Occurrence and activity of American martens *Martes americana* in relation to roads and other routes. Acta Theriologica 45:137–143.

Salas, D., J. Stevens, and K. Schulz. 2005. Rocky Mountain National Park, Colorado 2001–2005 vegetation classification and mapping. Remote Sensing and GIS Group, Technical Service Center, Bureau of Reclamation, Denver, Colorado, Final Report, Technical Memorandum 8260-05-02:1–145.

Slauson, K. M. 2003. Habitat selection by American martens (*Martes americana*) in coastal northwestern California. M.S. thesis, Oregon State University, Corvallis.

Smith, A. C., and J. A. Schaefer. 2002. Home-range size and habitat selection by American marten (*Martes americana*) in Labrador. Canadian Journal of Zoology 80:1602–1609.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management 47:1181–1186.

Streeter, R. G., and C. E. Braun. 1968. Occurrence of pine marten, *Martes americana*, (Carnivora: Mustelidae) in Colorado alpine areas. Southwestern Naturalist 13:449–451.

Taylor, S., and S. Buskirk. 1994. Forest microenvironments and resting energetics of the American marten *Martes americana*. Ecography 17:249–256.

Thomas, J. W., L. F. Ruggiero, R. W. Mannan, J. W. Schoen, and R. A. Lancia. 1988. Management and conservation of old-growth forests in the United States. Wildlife Society Bulletin 16:252–262.

Tyre, A. J., H. P. Possingham, and D. B. Lindenmayer. 2001. Matching observed pattern with model process: can territory occupancy provide information about life history parameters? Ecological Applications 11:1722–1737.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys by estimating false negative error rates in presence–absence data. Ecological Applications 13:1790–1801.

Weir, R. D., and A. S. Harestad. 2003. Scale-dependent habitat selectivity by fishers in south-central British Columbia. Journal of Wildlife Management 67:73–82.

Wilbert, C. J., S. W. Buskirk, and G. Gerow. 2000. Effects of weather and snow on habitat selection by American martens (*Martes americana*). Canadian Journal of Zoology 78:1691–1696.

Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. Journal of Wildlife Management 69:905–917.

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