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Season affects many characteristics of populations and, as a result, the interpretations of surveys conducted at different seasons. We explored seasonal variation in occupancy using data from four studies on the Pacific marten *Martes caurina*. Detection surveys were conducted during winter and summer using either cameras or track stations. We conducted a 'multiple location, paired season' analysis using data from all four study areas and a 'multiple season' analysis using seasonally replicated occupancy data collected at one of the areas. In the former analysis, summer occupancy estimates were significantly lower than winter and per visit probabilities of detection were indistinguishable between seasons. The probabilities of detection for the complete survey protocol were high (0.83 summer, 0.95 winter). Where summer and winter surveys were replicated, probability of occupancy was > 5 times higher in winter (0.52) than summer (0.09). We considered the effect of seasonal variation in occupancy on the habitat models developed using summer and winter survey data. Using the same habitat suitability threshold (0.5), the weighted average of winter models predicted significantly more suitable habitat than summer models. The habitat predicted by the summer model was at higher elevation, and was distributed among more, and smaller, patches of habitat than the model developed using winter data. We expect a similar magnitude of differences if summer or winter data were used to monitor occupancy. The higher occupancy in winter is probably due to the abundance of young animals detected during dispersal. Summer survey results reflect the distribution of territory-holding adults, thus these surveys may reliably detect breeding individuals and represent reproductive habitat. The implications of season on the interpretation of survey results, and corresponding habitat models and monitoring programs, provide a challenge to managers that make decisions about habitat management for martens, and other species with disparate occupancy among seasons.

The life histories and behaviors of animals that live in temperate environments have evolved with the influence of significant seasonal changes. Transitions from summer to winter conditions result in some obvious behavioral adaptations that include migration and hibernation. Demographic events also are adapted to seasonal changes, such that reproduction and dispersal occur during the most appropriate seasons. These events affect the seasonal movements and distribution of animals on the landscape and, presumably, our ability to detect them when we conduct surveys for their occurrence. For example, the amount of total activity of female mammals can increase significantly during the season when caring for dependent young (Powell and Leonard 1983, Henry et al. 2002). Increased activity translates to greater travel area, which can result in increased detectability during surveys for a species' occurrence. Thus, the detectability of demographic subsets of the population can vary with their reproductive status. Moreover, abundance and, therefore, detectability can be highest during the season when young disperse, which is late fall and winter for most species of temperate carnivores. The presence of juvenile animals not only elevates the population size, which will increase detectability (Smith et al. 2007), but these naïve individuals may be more easily attracted to baited locations where they can be detected. Maternal and dispersal behaviors can influence the relative distribution, and detectability, of individuals within populations of carnivores and these behaviors vary seasonally.

Seasonal variation in habitat use and energy expenditure has been described for many species of mammals. Rarely, however, has seasonal variation in survey results been accounted for by managers when developing monitoring

plans or interpreting the results of habitat models (Nielsen et al. 2010). When season is considered in designing an index of population size or exploring variation in probability of detection, it is often revealed as a critical component (Forsyth et al. 2005, Hackett et al. 2007, Slauson et al. 2012). Most commonly, managers consider only whether the target species occurred in an area, not when it occurred there, nor its sex or age. Yet these characteristics are essential in interpreting the meaning of a detection, when it is a datum in a habitat modeling exercise or a in a population monitoring program.

The Pacific marten *Martes caurina*, formerly the American marten *M. americana* in western North America (Dawson and Cook 2012), is a member of the weasel family (Mustelidae) and is associated with structurally complex, upper montane, late-seral coniferous forests (Spencer et al. 1983, Buskirk and Powell 1994, Payer and Harrison 2003, Zielinski et al. 2005). Martens are considered sensitive to habitat fragmentation (Bissonette et al. 1997), but they appear to tolerate some forms of forest management and other disturbances (Baker 1992, Zielinski et al. 2008, Koen et al. 2012). Seasonal variations in habitat use and in energy expenditure have been demonstrated for martens (Buskirk and Harlow 1989). Moreover, the effect of season of survey has been suggested as a factor that confounds the interpretation of marten habitat models. Kirk and Zielinski (2009) developed a landscape habitat model for martens using survey data collected during the summer and fall but found that it did not perform well when evaluated against survey data collected in the same region, but during the winter. Model accuracy improved when evaluation data were limited to summer and fall, strongly indicating potential differences in seasonal distributions of martens.

We explore this phenomenon more broadly in this paper, by reviewing seasonal variation in occupancy using data from four field studies. Three of the four were conducted for other purposes but used standard methods to conduct surveys for martens, comparing survey data collected during the summer and winter. Collectively, they provide a unique opportunity to understand the effect of season on detection and occupancy. We then consider the effects of season of survey when data are used to construct a habitat suitability model. Our goal is to describe seasonal variation in occupancy rates for martens at four study areas in California and to interpret how these results affect the decisions managers make about the type of data that are most appropriate for modeling marten habitat.

Methods

Detection surveys

We evaluated data from marten surveys conducted during the snow and snow-free periods of the year at four study areas on public lands in California: the High Sierra Ranger District of the Sierra National Forest ('High Sierra'), Lake Tahoe Basin Management Unit ('Tahoe'), Sagehen Experimental Forest on the Tahoe National Forest ('Sagehen'), and Lassen National Forest ('Lassen') areas (Fig. 1). The High Sierra and Tahoe study areas were replicates in a study designed to explore the year-round effects of off-highway vehicles on martens (Zielinski et al. 2008). The Sagehen study evaluated historical seasonal surveys over a 28-year period to help understand a regional marten population decline (Moriarty et al. 2011), and the Lassen area included three distinct study sites that were surveyed for the specific purpose of exploring seasonal variation in occupancy and its implications on habitat modeling and population monitoring.

All four studies used methods in which martens were attracted to chicken bait and olfactory lure for the purpose of detecting them at different seasons of the year. At Sagehen and Lassen the seasons were originally categorized as 'snow' versus 'snow-free' whereas in High Sierra and Tahoe the data were distinguished by the four astronomical seasons. However, we consider only surveys from each area that occurred from late June to mid-September, and from late-December to mid-April, which we refer to hereafter as 'summer' and 'winter', respectively. These seasons largely coincide with the periods of the year when there is either no snow, or abundant snow on the ground, respectively. We surveyed for martens using either enclosed track stations (Ray and Zielinski 2008) or remotely triggered cameras (Kays and Slauson 2008). Rectangular track stations were used at Sagehen, High Sierra and Tahoe during the summer. Tree-mounted camera stations were used during the winter at Sagehen, High Sierra, Tahoe, and during both seasons at Lassen. All track stations were placed on the ground, which is why they were not used during the winter when deep snow can cover them. Cameras were mounted from 2–4 m above the ground, depending on depth of snow. Characteristics of the survey methods used at each of the four study areas are described below and summarized in Table 1.

Sagehen
A total of 32 single station sample units were surveyed in summer 2007 and winter 2008. Surveys occurred in an approximately 35 km² area in the Sagehen Creek watershed, and seven sample units were in the adjacent Webber Lake watershed. The original summer surveys included 116 sample units (Moriarty et al. 2011), but the analysis here was restricted to the 32 sample units locations that were sampled in summer and in winter. Spacing of the sample units was on a 1000 × 1000 m grid, with the exception of the seven in the Webber Lake watershed which were on four linear routes with stations separated by an average of 1800 m. Track stations and cameras were checked and rebaited four times, every 6–8 days for a minimum of 35 operational days. Moriarty et al. (2011) includes more details on survey methods and study area.

High Sierra and Tahoe
The survey grids at High Sierra and Tahoe were each composed of 2-km² sample units (n = 46 at High Sierra and n = 48 at Tahoe). Each sample unit had multiple stations at least 250 m apart (three track stations in the summer and fall, two cameras in winter and spring) that were checked four times (once every 2–3 days for a minimum of 12 operational days) if they were tack stations and three times (once every 5–7 days for a minimum of 21 operational days) if they were cameras. This produced what we believed to be equivalent effort by season for the two methods (i.e. 3 track plates × 12 days = 36 effective 'survey days', 2 cameras × 21
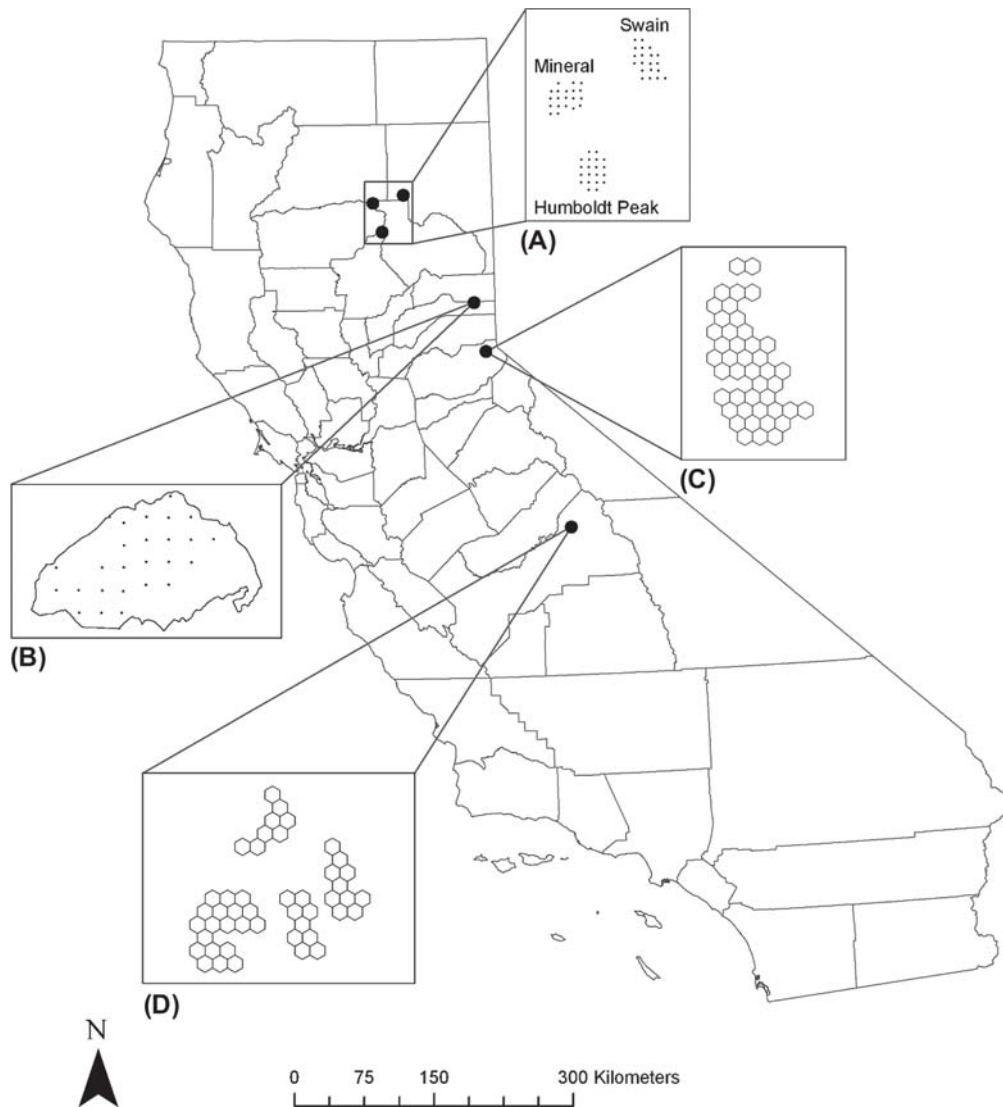
Figure 1. The location of the four marten study areas in California where work was conducted from 2003–2010. From north to south: Lassen (A), Sagehen (B), Tahoe (C), and High Sierra (D).

days = 42 'survey days'). Data were collected during four seasons each year, but only the data from summer (2003 Tahoe, 2005 High Sierra) and winter (2004 Tahoe, 2005 High Sierra) periods were used. Zielinski et al. (2008) includes more details on survey methods and the study areas.

Lassen

Unlike the other study areas, which were each a single grid of sample units, Lassen had three independent survey grids,

separated by at least 20 km from one another, referred to as Humboldt Peak, Swain and Mineral (Fig. 1). Thus, these were treated as three separate sites for the purpose of this analysis, particularly for examining change in occupancy by season over multiple years. Each grid used 20 single-camera station sample units each placed 3 km apart. Cameras were checked four times per season, once every 6–8 days for a minimum of 28 operational days. The Mineral grid was sampled twice (summer 2007, winter 2008) whereas Swain and Humboldt

Table 1. Survey devices and characteristics of survey methods used at each study location.

Study area	Bait/lure	Type of detection device		No. devices per sample unit		No. checks/days between checks		Effective survey days per sample unit[1]	
		Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
Sagehen	chicken/gusto[2]	track plate	camera	1	1	4/6–8	4/6–8	~35	~35
High Sierra	chicken/gusto	track plate	camera	3	2	4/2–3	3/5–7	~36	~42
Tahoe	chicken/gusto	track plate	camera	3	2	4/2–3	3/5–7	~36	~42
Lassen	chicken/gusto	camera	camera	1	1	4/6–8	4/6–8	~28	~28

[1]effective survey days = (number of devices in the sample unit) × (number of survey days device was functional)
[2]olfactory lure

Peak were sampled five times each (during three summers [2007, 2008, 2010] and two winters [2008, 2010]).

When cameras were used, a detection was defined as any photograph of a marten recorded within the time period between checks of the camera by a field technician. Cameras were used in either 2-station sample units (High Sierra, Tahoe) or single-station sample units (Sagehen, Lassen). When the former, a marten photograph at either of the cameras during a visit was considered a detection for the entire sample unit for that visit. Using track plates, a detection was defined as a confirmed marten track recorded within the time period between checks by the field technician. Track plates were deployed in either a 3-station (High Sierra and Tahoe) or 1-station (Sagehen) sample unit. When the former, a marten track at any one of the track stations in a sample unit during a visit was considered a detection for the entire sample unit for that visit.

On the Lassen study area, where we did the most comprehensive work, we used the same detection device (camera) for all winter and summer sample periods. In the other study areas, sample units were comprised of one or more track plates in the summer and one or more cameras in the winter, primarily due to the fact that track stations were available and the less expensive option for the summer. Martens typically have high probabilities of detection if present, for both track stations and cameras (Bull et al. 1992, Kirk and Zielinski 2009, Slauson et al. 2007, Zielinski et al. 1997). Also, when track stations were used, they were checked and rebaited more frequently than cameras because the bait can be removed more easily from track stations. This made the survey effort represented by track plate and camera surveys more equivalent. Finally, regardless of which detection method was used, the same bait and lure were used in summer as in winter.

Modeling occupancy

We conducted two separate analyses, the first took advantage of data from all four study areas and used the results from the first summer and winter season from each area. This analysis took advantage of spatial replication with the goal of exploring the consistency of the seasonal effect across multiple geographic locations. We refer to the first analysis as the 'multi-location, paired seasons' analysis. The second analysis focused on the results from Lassen only where there were replicates on season at two of the three sample grids (Humboldt Peak and Swain) allowing the fitting of a multiple season model where occupancy in season i depends on occupancy in season $i − 1$. We refer to this analysis as the 'Lassen multiple season' analysis and, although it focuses on a single location, its strength is the replication of survey data across multiple years.

Multi-location, paired seasons analysis
We fit a two-season model with the following Markov chain structure. We assumed that the probability of occupancy in the winter (season 2) depends on the true occupancy status in the summer (season 1). If we label the true occupancy status for season i as X_i and the number of observed detections with v_i visits for season i as Y_i, then this model can be defined in the following manner:

$$\Pr(X_1 = 1) = \psi_1$$
$$\Pr(X_2 = 1 \mid X_1 = 0) = \gamma$$
$$\Pr(X_2 = 0 \mid X_1 = 1) = \varepsilon$$
$$\Pr(Y_i = 0 \mid X_i = 0) = 1$$
$$\Pr(Y_i = y \mid X_i = 1) = \binom{v_i}{y} p_i^y (1 - p_i)^{v_i - y} \quad y = 0, 1, \ldots, v_i$$

$$p_i = p_{\text{Summer if } i = 1}$$
$$= p_{\text{Winter if } i = 2}$$

where ψ_1 is occupancy in the summer, γ is a colonization parameter (the probability that a sample unit becomes occupied between seasons), ε is an extinction parameter (the probability that a sample unit becomes unoccupied), and p_i is the probability of detection on a single visit. Occupancy during the winter (ψ_2) is defined (MacKenzie et al. 2006: 199) as:

$$\psi_2 = \psi_1 (1 - \varepsilon) + (1 - \psi_1) \gamma$$

We fit a separate set of parameters (ψ_1, ε, γ, p_{Summer}, and p_{Winter}) for each of the four study areas except we made the simplifying assumption that the probabilities of detection for each season (but not for both seasons) were the same for Sagehen and Lassen. This was necessary because of the few detections at Sagehen but it also seemed reasonable because marten populations at Lassen and Sagehen, in the northern portion of the range in California, appear to have more in common due to their proximity and the habitat changes to which they have been exposed (Zielinski et al. 2005, Moriarty et al. 2011), compared to populations in the southern portion of the range. Using the relationships described above, we calculated the likelihood contribution for each surveyed site and, from the sum of the log of the products of those likelihoods, determined the estimates that maximized likelihood for each parameter.

Lassen, multiple season analysis
The multiple season model was defined similarly to the multiple location, paired season model with the exception that season was replicated and indexed to reflect the chronological order of sampling, i.e. $i = 1, 3, 5$ for summers 2007, 2008 and 2010 and $i = 2, 4$ for winter of 2008 and 2010:

$$\Pr(X_1 = 1) = \psi_1$$
$$\Pr(X_i = 1 \mid X_{i-1} = 0) = \gamma_{i-1}$$
$$\Pr(X_i = 0 \mid X_{i-1} = 1) = \varepsilon_{i-1}$$
$$\Pr(Y_i = 0 \mid X_i = 0) = 1$$
$$\Pr(Y_i = y \mid X_i = 1) = \binom{v_i}{y} p_i^y (1 - p_i)^{v_i - y} \quad y = 0, 1, \ldots, v_i$$
$$p_i = p_{\text{Summer}} \text{ if } i = 1, 3, 5$$
$$= p_{\text{Winter}} \text{ if } i = 2 \text{ or } 4$$

Note that ψ_i for $i = 2, 3, 4, 5$ we have

$$\psi_i = \psi_{i-1} (1 - \varepsilon_{i-1}) + (1 - \psi_{i-1}) \gamma_{i-1}$$

Note also that there is a longer gap between sample $i = 3$ and 4 than between the other sample periods which is due to absence of sampling during the winter of 2009 (see also Fig. 2). This will affect estimates of γ (colonization parameter) and ε (extinction parameter), which estimate the gain and loss, respectively, of occupancy at sample units. If similar to the effect of sporadic sampling on extinction and
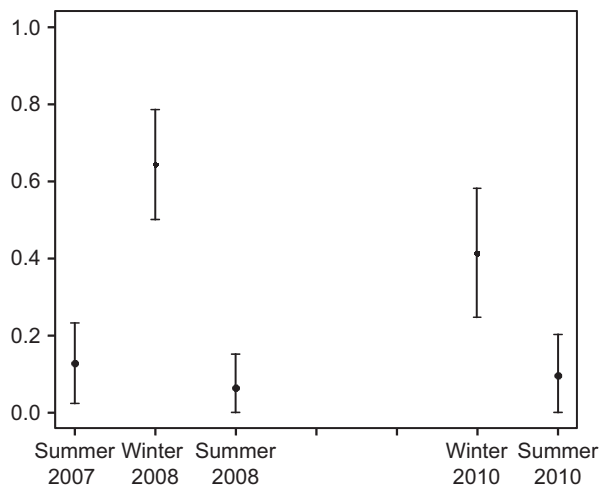
Figure 2. Estimates of the probability of occupancy for the three summers (2007, 2008 and 2010) and two winter (2008 and 2010) marten surveys at the Lassen study area. Vertical bars represent 95% confidence intervals. The gap in the x-axis represents temporal gap in sampling.

immigration on islands, this gap in temporal continuity of sampling may result in underestimates of turnover rates (Clark and Rosenzweig 1994). All parameter estimates were achieved using maximum likelihood methods, as described above for the multiple location, paired seasons analysis. In both analyses we used the delta method (Bishop et al. 1975) to estimate standard errors and confidence intervals for the purpose of comparing the parameters.

Habitat modeling

We sought to determine the differences in habitat models, and their resulting maps of habitat suitability, that would occur when using summer versus winter survey data. Detection and non-detection data from marten surveys (1992–2008) were provided by the Lassen National Forest. Most of these surveys were conducted at sites where some kind of land management activity was proposed. Records were deleted that had insufficient data (e.g. poor location data, suspect species identification) or for surveys that were at elevations below where most marten locations typically occur (< 1219 m [4000 ft] Zielinski et al. 1997). This left a balance of 753 records of 122 detections and 631 non-detections. The data were very spatially clustered, with small (most < 2400 m) nearest-neighbor distances. To select survey points more likely to be independent, a spatial filter was applied to exclude one of a pair of points that were within 300 m, resulting in a summer dataset of 364 records (22 detections and 342 non-detections) and a winter dataset of 425 records (99 detections and 326 non-detections).

A wide array of abiotic and biotic potential predictor variables were derived from Geographic Information System (GIS, ESRI ArcMap 9.3) data layers at 900-m^2 resolution (30 × 30 m) (Supplementary material Appendix 1). We applied a moving window to average predictor variables over a 0.25 km^2 assessment area centered on each survey location. Vegetation data used to derive all biotic variables were provided by the Lassen National Forest or, outside the

national forest we used USFS EVEG Tiles (USDA Forest Service, Pacific Southwest Region, Remote Sensing Laboratory, Existing Vegetation tiles, 2005–2009). Landscape variables were derived using the software program FRAGSTATS (ver. 3.3; McGarigal et al. 2002).

We created 227 candidate models using different combinations of environmental predictor variables presumed to influence marten occurrence. This set included many evaluated also by Kirk and Zielinski (2009) plus some additional ones that were possible because of new variables available to us. All models, however, were created based on perceived ecological relationships between marten occupancy and multivariate habitat relationships. The variables were grouped into six 'families' (climate, topography, cover type, tree size and density, management and landscape arrangement) and models were created using variables from within and between the families. Because the probability of detections for martens, in our study and elsewhere (Slauson et al. 2007, Kirk and Zielinski 2009) is close to 1, for the purposes of this demonstration we used logistic regression to model marten probability of occurrence (R ver. 2.9.2). Candidate models were compared statistically to determine which model(s) best fit using AIC weights (w) corrected for small sample size (AIC$_c$) (Burnham and Anderson 2002). Candidate models within < 2 AIC$_c$ units of the best-fitting model were averaged to create the final model. Averaging was conducted by using the sum of each model's prediction multiplied by its AIC$_c$ weight.

Results

Multi-location, paired seasons analysis

Estimated summer occupancy rates were significantly lower than winter rates (Wald test, p < 0.02) (Table 2). The magnitude of the seasonal difference in estimated occupancy (winter minus summer) was greatest at Lassen (0.48) and least at the High Sierra (0.11). Per visit probabilities of detection (p) in winter were statistically indistinguishable from those in summer (Wald test, p = 0.33) ranging from a low of 0.23 in the summer in Lassen and Sagehen to a high of 0.83 in the summer at High Sierra (Table 2). The probability of detection at a single sample unit over the course of an entire survey (P) is calculated by compounding the per visit probability of detection (p) by the number of visits (v): $P = [1 - (1 - p)^v]$. These values were uniformly high (mean = 0.83 and 0.95 in summer and winter, respectively) ranging from a low of 0.66 in Lassen and Sagehen in the summer to a high of > 0.99 in the High Sierra in both seasons and in Tahoe in summer (Table 2). Thus, the spatial and temporal characteristics of our survey methods assured high probabilities of detecting martens when they were present at a sample unit.

Lassen, multiple season analysis

When seasonal surveys were replicated (three summers and two winters) at the same locations, the estimated probability of occupancy was also significantly greater in winter than in summer (Table 3, Fig. 2). Mean estimated occupancy was significantly greater in winter (0.52) than summer (0.09)

Table 2. Estimates of occupancy (ψ), differences in occupancy, and probabilities of detection per visit (*p*) and for the full multi-visit protocol (*P*) for the four study areas in California using the multiple location, single season analysis. Summer data collected in 2007, 2008 and 2010 at Lassen and 2005, 2004 and 2007 at High Sierra, Tahoe and Sagehen, respectively. Winter data collected in 2008 and 2010 at Lassen and in 2005, 2005, and 2008 at High Sierra, Tahoe and Sagehen locations, respectively.

Study area	Occupancy summer $\hat{\psi}_{Summer}$	95% CI	Occupancy winter $\hat{\psi}_{Winter}$	95% CI	Difference: Winter – Summer Difference	95% CI	Summer detection probability per visit (*p*) (95% CI)	Winter detection probability per visit (*p*) (95% CI)	Summer detection probability for full protocol (*P*) (95% CI)	Winter detection probability for full protocol (*P*) (95% CI)
Lassen	0.15	(0.01, 0.30)	0.64	(0.49, 0.78)	0.48	(0.30, 0.67)	0.23 (0.02, 0.45)	0.44 (0.35, 0.52)	0.66 (0.27, 1.00)	0.90 (0.84, 0.96)
High Sierra	0.89	(0.80, 0.98)	1.00	not estimable	0.11	(0.02, 0.20)	0.83 (0.77, 0.89)	0.79 (0.72, 0.86)	1.00 (1.00, 1.00)	1.00 (1.00, 1.00)
Tahoe	0.75	(0.61, 0.88)	0.95	(0.83, 1.00)	0.20	(0.04, 0.37)	0.66 (0.58, 0.75)	0.74 (0.64, 0.84)	0.99 (0.97, 1.00)	1.00 (0.99, 1.00)
Sagehen	0.05	(0.00, 0.14)	0.24	(0.08, 0.40)	0.19	(0.03, 0.35)	0.23 (0.02, 0.45)	0.44 (0.35, 0.52)	0.66 (0.27, 1.00)	0.90 (0.84, 0.96)

(Wald test, $p < 0.0001$). Extinction rates were highest for the two transitions from winter to summer (0.77 and 0.90) and colonization rates highest for the two transitions from summer to winter (0.40 and 0.59) (Table 3). As was the case for the multiple location analysis, probabilities of detection were statistically indistinguishable in summer versus winter (Wald test, $p = 0.08$, Table 3).

Habitat modeling

Summer
The highest ranking marten occurrence model developed using the summer survey data (model 215) accounted for 17% of the Akaike weight (Table 4). Five additional models were within 2.0 AICc units of this model (models 152, 182, 193, 142 and 162). Together these six models accounted for 67% of the Akaike weight and were averaged to produce a model that was used to create a summer habitat suitability map (Fig. 3). All of these models included elevation (ELEV) and the majority include distance to water (WATERDIST) as predictors, suggesting the role of cool and mesic habitat features. Two of the top models also indicated the importance of lodgepole pine (LPN).

Winter
The highest ranking marten occurrence model developed using survey data from the winter (model 137) accounted for 10% of the Akaike weight (Table 4). Nine additional models were within 2.0 AICc units of this model, so the top ten models were averaged. Together these models accounted for 69% of the Akaike weight and produced a model that was used to create habitat suitability map for the winter (Fig. 4). As in the summer, all the top winter models included elevation (ELEV) as a predictor but unlike the summer models they all also included precipitation (PRISM). Several of the top winter models included variables that reflected medium/large tree classes (MDLG_RFR, MDLG_FOR); variables which were absent from the top summer models.

The weighted average of the models from the winter surveys (Fig. 4) predicts significantly more area to have high probability of occupancy, compared with the models created from the summer survey data. Using > 50% probability of predicted occurrence as a threshold to define suitable habitat, nearly four times as much suitable habitat is predicted for the winter than the summer. Suitable habitat predicted by the averaged summer model is constrained to smaller patches at somewhat higher elevations than the averaged winter model. Mean elevation for suitable habitat predicted by the summer model is 2,256.7 m ± 155.4 SD, compared to 2,073.5 ± 176.4 for the winter model. The distribution of patch sizes also had a pronounced seasonal difference, with the summer model characterized by more, smaller patches of habitat above the threshold level (Fig. 5). The dominant cover type for both summer and winter models was red fir, comprising 46% of predicted suitable summer habitat and 36% of predicted suitable winter habitat. Discrepancies between the models also included the amount of 'barren' habitat in the summer than winter (12% summer, 6% winter) and more lodgepole pine in the summer (9%) than winter (5%), both differences reflecting the higher elevations predicted as marten habitat in the summer.

Table 3. Estimates of occupancy (ψ), probability of detection (*p*), extinction (ε) and colonization (γ), and their standard errors for the five surveys used in the Lassen, multiple season analysis. ne = not estimable.

Parameter	Summer 2007	Winter 2008	Summer 2008	Winter 2010	Summer 2010
ψ	0.13 (0.05)	0.64 (0.07)	0.06 (0.04)	0.41 (0.09)	0.10 (0.05)
p	0.32 (0.09)	0.42 (0.04)	0.31 (0.09)	0.42 (0.04)	0.32 (0.09)
ε	–	0.00 ne	0.90 (0.07)	0.40 (0.39)	0.77 (0.13)
γ	–	0.59 (0.08)	0.00 ne	0.40 (0.09)	0.00 ne

Discussion

The collective results from studies in four separate locations in California support the hypothesis that estimated marten occupancy is significantly greater during winter than summer. This is unrelated to differences in probability of detection, given that existing protocols detect a marten that is present at rates that were typically > 90% (the summer period estimated jointly for Sagehen and Lassen was an exception). Our protocols for detecting martens were very effective, revealing a significantly lower occupancy in summer than in winter. This has important implications for the interpretation of survey results: if a survey is conducted in winter, our results suggest that there is a much better chance of confirming occupancy than if the survey is conducted in summer, other factors being equal. This seasonal difference is not due to differences in probability of detection if present (*p*), which were equivalent in summer and winter, but instead due to differences in estimates of occupancy. This result means that the choice of survey season can affect conclusions about how management decisions are made, and how martens and their habitat are affected. If, for example, the goal is to err on the side of caution and to conduct a survey with the greatest chance of a detection, a winter survey would be recommended. And, if a detection results in some form of habitat protection at the site, then winter surveys may lead to the protection of a greater amount of habitat. Conversely, summer surveys, will have a lower chance of detecting a marten at the same survey location resulting in a different outcome and, perhaps, a different management decision.

The choice of when to conduct the survey can also be influenced by what a detection means in respect to the separate demographic components of the population. A summer survey is more likely to detect an adult, resident individual than a young dispersing juvenile. Although adult males may make movements during this time, summer is generally outside the dispersal season. Because adult residents have more effect on population health and growth, the results of summer surveys may more faithfully represent the status of the core of the breeding population. Summer surveys may also be able to distinguish sexes, if they are conducted using track surveys (Slauson et al. 2008) or genetic sampling (Schwartz and Monfort 2008), and can therefore identify the detections of females, the most critical component of the population. Conversely, although winter surveys may have a greater probability of confirming occupancy, this is most likely due to the influence of abundant young-of-the-year animals on occupancy estimates. Thus, winter surveys may produce more optimistic outcomes, in terms of occupancy, but they may not be as useful to monitoring population status because of the disproportionate influence of young animals, many of which may never contribute to the breeding population. Work is underway to determine the age and sex classes of martens detected during each season (Zielinski and Moriarty unpubl.) as this will be necessary to confirm these predictions.

We also demonstrated the significant effect that season of survey data has on the development of empirical models of landscape habitat suitability. Summer survey data yield a habitat model that identifies habitat at higher elevation, with different predictors and greater number of smaller patches of predicted habitat than does a model developed using winter survey data. Thus, the choice of season of survey data can also influence the type of information about marten habitat provided to managers. Winter survey data resulted in the most liberal view of the amount of habitat whereas summer data resulted in a model that identified a smaller total amount of predicted habitat, which was also more fragmented and at higher elevation. Moreover, the fewer habitat patches that are identified by the summer model may each be perceived as more critical to maintain if they represent areas used primarily by adults in the breeding population. Models built from summer surveys are likely to correspond to the habitat of the core breeding population whereas winter surveys are more likely to identify a larger area, and perhaps a greater diversity of habitats reflecting the less discriminating choices made by young, dispersing animals (Stamps 2001).

Kirk and Zielinski (2009) were the first to realize that survey season affected the predictive power of marten habitat models. Their models built using only summer survey data were poor at predicting winter detection results. Kirk and Zielinski (2009) were unaware of the significant differences in occupancy that we have demonstrated here. However, they hypothesized that summer habitat may be more limiting to martens and that during winter martens may: 1) shift or expand their home ranges downslope into a broader range of habitat conditions, or 2) that these winter expansions represent dispersing individuals that were unable to establish a home range in higher elevation habitats that are occupied year-round by resident animals. It is also possible that with resources more abundant in the summer, home ranges may contract when compared to winter. There is some evidence for the seasonal change and expansion of home ranges in martens (O'Doherty et al. 1997, Zalewski et al. 2004) and other carnivores (Whitman et al. 1986, Bixler and Gittleman 2000, Grigione et al. 2002) so that is a possibility. However, shifts in home range location and size appear to differentially affect male martens more than females and be related to movements made by males during the breeding season (Phillips et al. 1998). Because fall and winter marten populations are larger due to the addition of young-of the-year

Table 4. Top-ranked models for each season, number of model parameters (K), ΔAIC values, AIC weights (w_i), model likelihood and the mean and standard deviation of the area under the curve (AUC) of the receiver operating characteristic (ROC) function under cross validation (CV). Data collected at Lassen National Forest from 1992–2008.

Season	Model no.	Model	K	ΔAIC_c	w_i	Model likelihood	Mean 5-fold CV ROC AUC
Summer	215	$-20.43 + 2.7(MDLG\_FOR) - 0.01219(GYRATE\_AM) + 4.398(PLANTATION) + 0.01008(ELEV) - 0.001222(WATERDIST)$	6	0.00	0.17	1.00	0.86
	152	$-16.75 + 4.583(LPN) + 0.006592(ELEV) + 0.00001162(PRISM) - 0.6164(STRMDEN)$	5	0.55	0.13	0.76	0.89
	182	$-21.52 + 0.002023(STRUCT) - 0.01377(GYRATE\_AM) + 4.433(PLANTATION) + 0.0106(ELEV) - 0.001223(WATERDIST)$	6	0.93	0.11	0.63	0.88
	193	$-21.110 + 3.152(KHREPRO) - 0.01674(GYRATE\_AM) + 4.436(PLANTATION) + 0.01042(ELEV) - 0.001176(WATERDIST)$	6	1.17	0.10	0.56	0.88
	142	$-16.77 + 5.043(MDLG\_LPN) + 0.6634(ELEV) + 0.00001196(PRISM) - 0.6294(STRMDEN)$	5	1.61	0.08	0.45	0.89
	162	$-19.86 + 0.00003257(STRUCT) + 4.553(PLANTATION) + 0.009529(ELEV) - 0.001039(WATERDIST)$	5	1.68	0.07	0.43	0.89
Winter	137	$-12.62 + 1.374(MDLG\_RFR) + 0.005153(ELEV) + 0.00001531(PRISM) + 0.1929(STRMDEN)$	5	0.00	0.11	1.00	0.82
	147	$-12.440 + 1.001(RFR) + 0.005041(ELEV) + 0.00001538(PRISM) + 0.1954(STRMDEN)$	5	0.26	0.09	0.87	0.81
	142	$-13.76 + 3.477(MDLG\_LPN) + 0.005754(ELEV) + 0.00001595(PRISM) + 0.2149(STRMDEN)$	5	0.82	0.07	0.66	0.81
	218	$-12.56 + 1.477(MDLG\_FOR) + 0.049(NDCA) + 0.005095(ELEV) + 0.00001526(PRISM) + 0.1954(STRMDEN)$	6	0.89	0.07	0.64	0.81
	207	$-12.66 + 1.63(MDLG\_FOR) - 0.008056(PROX\_AM) + 0.00515(ELEV) + 0.00001548(PRISM) + 0.1949(STRMDEN)$	6	0.94	0.07	0.62	0.81
	212	$-12.69 + 1.685(MDLG\_FOR) - 0.0004382(GYRATE\_AM) + 0.005169(ELEV) + 0.00001555(PRISM) + 0.1957(STRMDEN)$	6	0.96	0.07	0.62	0.81
	129	$-12.45 + 0.6832(KHREPRO) + 0.005037(ELEV) + 0.000016(PRISM)$	4	1.01	0.07	0.60	0.80
	127	$-12.43 + 0.0004304(STRUCT) + 0.005022(ELEV) + 0.000016(PRISM)$	4	1.27	0.06	0.53	0.81
	152	$-13.59 + 2.085(LPN) + 0.005678(ELEV) + 0.00001574(PRISM) + 0.2035(STRMDEN)$	5	1.52	0.05	0.47	0.81
	157	$-12.94 + 0.0004325(STRUCT) + 0.005334(ELEV) + 0.000015(PRISM) + 0.2038(STRMDEN)$	5	1.64	0.05	0.44	0.80

individuals to the population and we think that this is the most likely reason for the seasonal differences in occupancy. This subject, however, needs additional research attention.

Our survey designs included three or four visits, which resulted in very high probabilities of detection (five of six mean estimates for the full protocol were > 0.9). Martens typically have high probabilities of detection (Kirk and Zielinski 2009, Slauson et al. 2012). Our high estimate of detection probability provided some insurance against bias in each of the parameters of interest (p, ψ) (McKann et al. 2013). Exceptions were the relatively low estimates of ψ and p at Lassen and Sagehen. However, if this led to bias in the summer in these areas it would be positive bias and would mean that we are being conservative when estimating the winter–summer difference, because there is little bias in the winter and winter estimates are higher than summer. And, although we did account for heterogeneity in our estimates of p by accounting for season and study area, we did not explore additional covariates. Our generally high values for p made this less necessary (Royle 2006). However, future work should consider increasing the number of sites, since bias in estimating occupancy is least when the number of sites > 60 (McKann et al. 2013).

We acknowledge that, in the multi-location analysis, to achieve the power of combining multiple data sets we had to make concessions in consistency in survey design. The four data sets were collected from survey designs that differed in the detection devices used and the number of devices per sample unit. Fortunately, as noted earlier, martens have high rates of detection and low latencies to first detection, rendering some of these differences less influential. Moreover, this caveat does not apply to the Lassen, multiple season analysis, where all aspects of survey protocols were identical in summer and winter. However, we recommend that future research on this topic, when combining data sets from multiple studies, attempt to standardize survey effort even more than was possible here. We also acknowledge that we have assumed closure in the population during the course of sampling occupancy during each season. We believe this is valid given the size of the study areas sampled, the relatively short duration of sampling, and the fact that the only change in marten home ranges appears to be by males during the breeding season (Phillips et al. 1998). If the assumption of closure is demonstrated in the future to be invalid, seasonal movement dynamics may need to be specified in modeling occupancy and probability of detection.

Finally, the analysis of the multi-location data revealed a pattern that was surprising, in that the difference in seasonal occupancy in each study area appeared to be related to how the region in which it occurred had been affected by forest management activities. The Lassen and Sagehen study areas demonstrated the greatest magnitude of difference between summer and winter occupancy whereas the High Sierra and Lake Tahoe study areas demonstrated more modest seasonal differences. Lassen and Sagehen are in the northern Sierra Nevada subregion, which a GAP analysis (Davis and Stoms 1996) revealed has only 1% of the area in Class 1 lands (public or private lands formally designated for conservation of biodiversity). This is in contrast to the central/ south Sierra Nevada subregion, where High Sierra and Lake Tahoe areas occur, which has 27% of the land area in lands
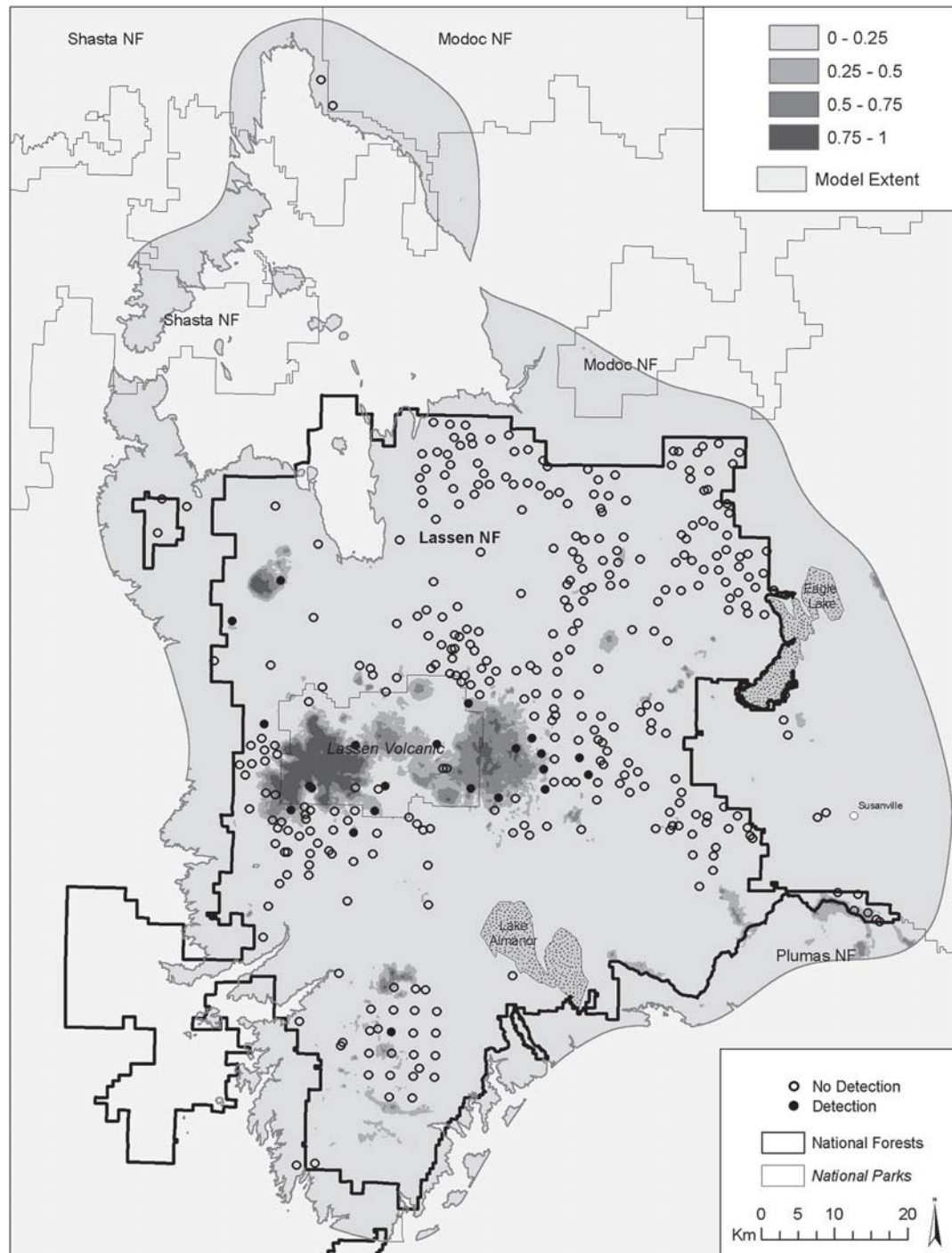
Figure 3. Predicted occupancy from the weighted average of top six models created from summer detection data, collected from 1992–2008, Lassen National Forest, California. Closed circles represent detections, open circles no detection.

classified as Class 1. The marten habitat in the Lake Tahoe and High Sierra study areas is at higher elevations, where there has been less disturbance by timber harvest. The possible link between history of disturbance and magnitude of seasonal difference in occupancy is speculative, and should be explored further, but it may be related to how demographic dynamics are affected by landscape habitat conditions. If, for example, a landscape is dominated by poorer quality habitat (as the result of timber harvest or forest thinning, for

example) there may be fewer opportunities for juveniles to establish breeding territories. Juveniles may arrive in these study areas from elsewhere, and make their presence known during winter surveys, but not establish residency (or survive) to be detected in the following summer. This would result in a significant discrepancy between summer and winter occupancy. Conversely, if a landscape includes an abundance of high value habitat then there may be more opportunities for year-round residency by occupants and,
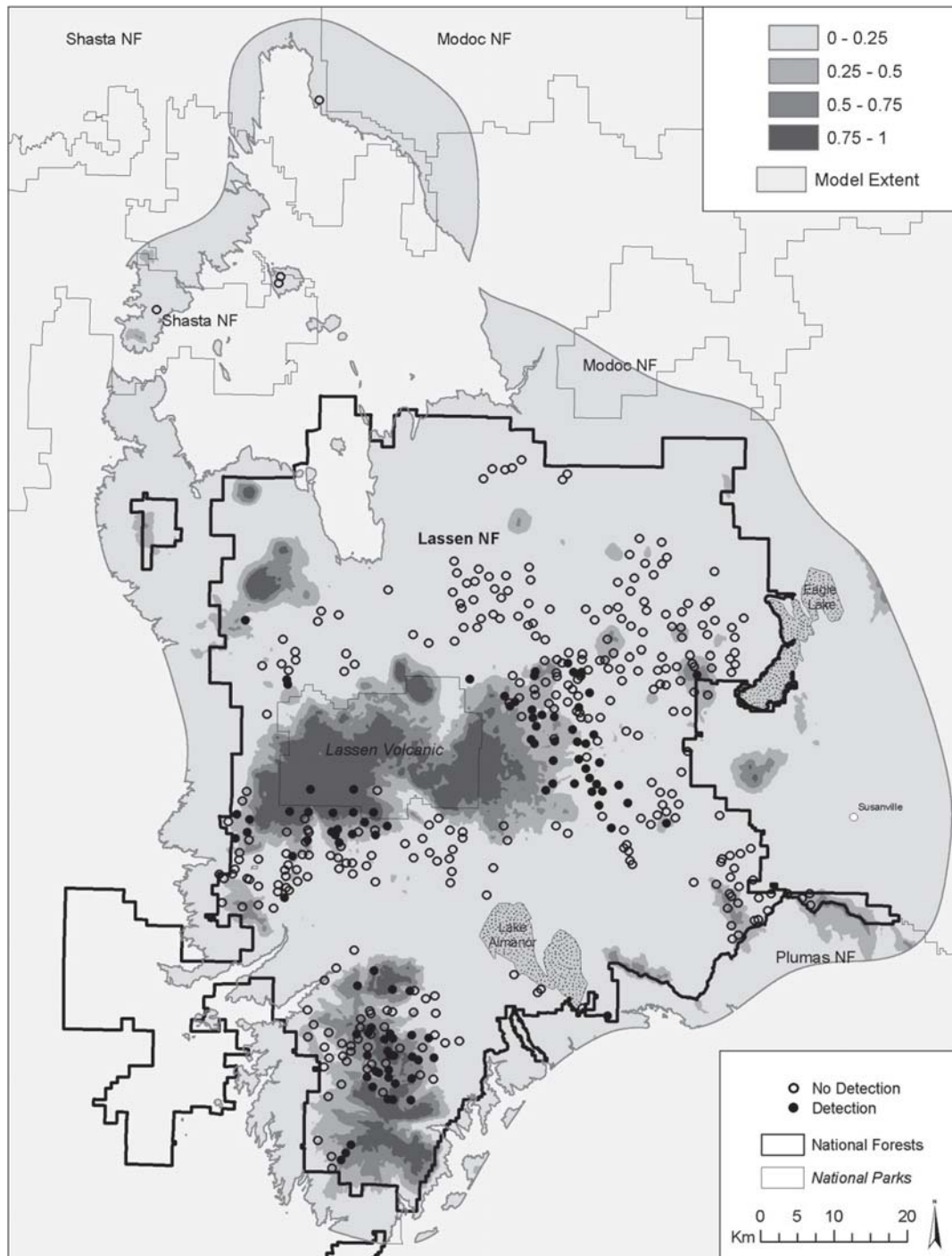
64

Figure 4. Predicted occupancy from the weighted average of top 10 models created from winter detection data, collected from 1992–2008, Lassen National Forest, California. Closed circles represent detection, open circles no detection.

thus, a less marked difference between occupancy between seasons, as we observed in these two areas.

In conclusion, the season of sampling affects estimates of occupancy which, in turn, affects the characteristics of the maps of predicted habitat that are produced. Forest managers may find very different amounts and distribution of habitat, depending on whether a summer or a winter model is used. Models built from summer surveys are likely to correspond to the habitat of the core breeding population

and it may be especially important to retain patches of core habitat identified by summer models, and the areas that connect them. These patches are less extensive and smaller than patches identified from winter survey data, and potentially more important. However, the locations identified by winter models are also important, given that the dynamics of marten persistence depend on the role of dispersing juveniles to find and occupy suitable, but currently unoccupied patches. For this reason we recommend that managers who are
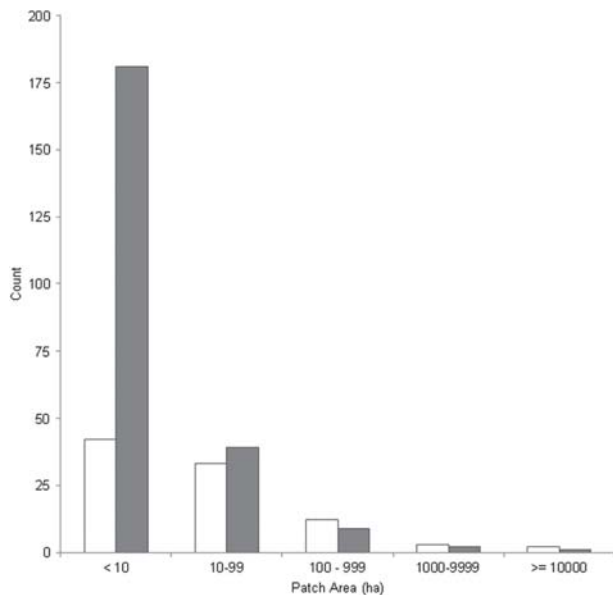
65

Figure 5. Distribution of patch sizes of predicted habitat, using a > 50% prediction threshold, for the summer (gray bars) and winter (white bars) models, Lassen National Forest, California. Field data for model development was collected from 1992–2008.

planning land management activities in marten habitat consider both summer and winter models to best understand their impacts to marten habitat.

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Supplementary material (available online as Appendix wlb.00077 at <www.wildlifebiology.org/readers/appendix>). Appendix 1.