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Using high-resolution short-term location data to describe territoriality in Pacific martens

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Solitary carnivores in the family Mustelidae are thought to exhibit pronounced intrasexual territoriality, defending space against competitors but tolerating members of the opposite sex. Although mustelids move long distances daily, how such movements reflect intrasexual territoriality is relatively unknown. We hypothesized that martens make regular movements around the boundaries of their territories and that territories typically would be stable across seasons and years. Consequently, we predicted that high-resolution movement data would reveal territorial boundaries within days to weeks. We collected movement data (from GPS collars) and long-term location data (from VHF collars) for 25 adult Pacific martens (*Martes caurina*) in 2 study areas (coastal and montane). We used GPS movement data to estimate utilization distributions and evaluate individual overlap and stability of territories between seasons, and compared those with annual home ranges from VHF locations. We also used incremental analysis to calculate how many days of movement data were required to fully describe a marten's territory. Marten territories estimated from GPS movement data were indistinguishable from annual home ranges (spatial overlap, $\bar{X} \pm SD$, 0.99 ± 0.13, $n = 9$) and remained relatively stable year-round with some expansion during winter. Territories of same-sex neighbors overlapped < 2%. Our models suggested that an individual marten's movements encompassed 95% of its territory within 2.25–14 days ($\bar{X} = 4.6$ days); that time did not differ between study areas, sexes, or seasons. Location data with high spatial and temporal resolution could enable more precise estimates of territoriality in this and potentially other carnivore species, and illuminate hitherto unobservable behavioral differences across time and space.

Key words: carnivore, home range, GPS collar, marten, *Martes americana*, *Martes caurina*, movement, mustelid, scent marking, territoriality

Population-level spatial organization is the outcome of decisions made by individuals that restrict movements, often to areas that are familiar, resulting in the formation of home ranges or territories (Brown and Orians 1970; Börger et al. 2008). The concept of home range, or area that fulfills an individual's needs over long periods (seasons to years—Burt 1943), is widely applied but may be particularly relevant to territorial carnivore species, where territories are the area of the home range that is actively defended (Burt 1943). In such cases, the territory may be indistinguishable from the home range (Brown and Orians 1970). Where animals are rigidly territorial, individuals may frequently travel within and along the perimeter of their home ranges to maintain or defend that territory (Zub et al. 2003), as expected when resources are limited (Wiens 1976). Evaluating movements associated with fitness-related behaviors such as food and mate acquisition and the defense of territories can inform understanding of population-level spatial organization (Spencer 2012). Thus, observing fine-scale movements at appropriate time scales may provide insights as to how individuals adapt to a stochastic and changing environment, and potentially how a population may respond to perturbations, such as shifts in climate, reductions in habitat, or disease (Walther et al. 2002; Potts et al. 2013).

Socio-spatial organization in carnivores arises from predictable decisions by individuals in their movements and space use, and can vary based on social group size, prey mobility, and reproductive strategy. As an example, carnivores in the mustelid (weasel) family are primarily solitary, and most direct social contact between adults occurs during a short breeding season in the spring or summer. Spatial organization in mustelids is predicted to form from intrasexual intolerance and defense, whereby same-sex adults restrict access to each other, and intersexual tolerance, where males overlap with several females (Erlinge 1979; Powell 1979, 1994). Generally, mustelids exhibit semi-exclusive intrasexual territories (e.g., Zalewski and Jędrzejewski 2006; Inman et al. 2012), with some exceptions (e.g., Rennie 2015). Yet, spatial organization may vary with resources. The degree to which animals are territorial may be predicted as a function of daily energetic requirements, cost of territorial defense and territory size, and food productivity (Carpenter and MacMillen 1976; Powell et al. 1997). Powell (1994) predicted that spacing patterns in mustelids should vary from exclusive to highly overlapping territories among same-sex neighbors along a gradient from low to high resource densities. Conversely, territoriality of individuals may remain constant but territory sizes may change depending on resources (Herr et al. 2009). Research on this subject could be improved with the ability of GPS telemetry to increase locations at a higher rate of intensity compared with the laborious nature of obtaining VHF telemetry locations with sufficient sampling to estimate a territory (Cagnacci et al. 2010).

Martens (*Martes* sp.) exemplify species for which a better understanding of movements and territorial behaviors could improve management and conservation. North American martens are forest-dependent mustelids (Spencer 1981; Buskirk and Powell 1994) that are active year-round, foraging daily to meet energy requirements (Iversen 1972) and consuming an equivalent of 20–30% of their body weight daily (Gilbert et al. 2009). Martens are adapted to hunt small, dispersed prey and move many times longer distances by body mass than either canids or felids (Goszczyński 1986). For example, Pacific martens (0.6–1.3 kg, *Martes caurina*) moved 6–7 km daily on average (Moriarty et al. 2016), similar to distances reported for bobcats (6–18 kg, *Lynx rufus*—Newbury 2013). Movements are typically restricted to areas with forest cover (Cushman et al. 2011; Moriarty et al. 2015) and the propensity of most martens to avoid openings translates into disproportionate absence of populations in fragmented landscapes (Hargis et al. 1999; Potvin et al. 2000; Fuller 2006). Martens may traverse familiar areas in short periods: for instance, pine martens (*Martes martes*) traversed > 75% of their territory in 3–10 days (Balharry 1993; Zalewski et al. 2004).

One reason for such rapid and extensive movements may be territorial defense, whether active (agonistic behaviors against other individuals) or passive (e.g., scent marks). Mustelids limit direct contact but use a diverse repertoire of chemical scent marks, likely in frequent communication (Buskirk et al. 1986). Olfactory scent marks have been hypothesized to be effective in communicating territory boundaries and social status of the territory owner to neighbors, with scent marks acting as a proxy for owner presence (Kruuk 1992; Gese and Ruff 1997; Sillero-Zubiri and Macdonald 1998; Potts et al. 2013), but those marks may not persist for more than a few days. Estimates of this duration for other mammals range from 3 to 5 days in red foxes (*Vulpes vulpes*—Potts et al. 2013), 7 days for klipspringer antelope (*Oreotragus oreotragus*—Roberts 1998), and 10 days for dwarf mongooses (*Helogale undulata rufula*—Rasa 1973).

For martens, territorial behaviors are not well understood, nor is it known whether territories are stable over long time periods (e.g., seasons and years). Whether territorial behaviors vary by sex and season is also unclear, although seasonal differences in prey densities and different reproductive trade-offs in males and females suggest males would have larger territories (Powell 1994) and both sexes would maintain similar territories year-round (Chapin et al. 1997; Phillips et al. 1998) or increase range size during spring and summer during the reproductive season (Zalewski and Jędrzejewski 2006).

We evaluated the hypotheses that adult Pacific martens make regular movements around the boundaries of their territories and that territories typically would be stable across seasons and years assuming there was no change in vegetation structure, prey populations, or population metrics (e.g., survival). Because of the apparently short duration of scent communication, we predicted individual martens would move rapidly and traverse the majority of their territories' boundaries within a time frame of days, rather than over the period of months as has typically been used for home range estimation. Specifically, we predicted that monitoring a marten's movement for a short period (e.g., < 10 days—Zalewski et al. 2004) would be sufficient to estimate accurately a seasonal, as well as an annual home range—providing a spatial depiction of population structure. We further predicted that territory size would vary by sex with ranges of males larger than those of females, and would not vary by season. We tested our predictions in 2 study areas by 1) comparing ranges estimated from GPS deployments that characterized fine-scale movements for < 5 weeks with size and location of annual home ranges encompassing > 8 months of VHF telemetry location data, and 2) evaluating spatial overlap of neighboring martens to estimate exclusive space use, which we inferred represents territorial spacing at the population level. Finally, we calculated the time over which Pacific martens moved through their entire territory, predicting the minimum number of hours necessary to describe territory size within our study populations would be similar to that reported for European marten populations (i.e., encompassing a period < 10 days—Balharry 1993; Zalewski et al. 2004), and would not vary by sex or season.

Materials and Methods

Study area.—This research was conducted in Lassen National Forest, California (hereafter, Lassen) and in the Oregon Dunes National Recreation Area, Oregon (hereafter, coastal Oregon). Our study area in Lassen was a montane

region in the southern Cascades range, with elevations that ranged from 1,500 to 2,100 m. Forest cover in the Lassen study area included red fir (*Abies magnifica*), white fir (*A. concolor*), lodgepole pine (*Pinus contorta*), mixed conifer, and riparian areas. Non-forest included perennial meadows, talus lava fields, and frozen lakes during winter. Mean minimum and maximum temperatures in July were 6.9°C and 29.5°C, respectively, and −6.9°C and 5.3°C in January (Western Regional Climate Center 2012). Winter mean annual snow depth was 134 cm (California Department of Water Resources 2012). Snow pack persisted in Lassen from December through May (winter season) and snow-free conditions were from June through November (summer season).

Elevations in coastal Oregon ranged from just above sea level (8 m) to 80 m. Forest cover consisted of shore pine (*Pinus contorta contorta*) and sitka spruce (*Picea sitchensis*) with an understory dominated by slough sedge (*Carex obnupta*) and willows (*Salix hookeriana*) in seasonally flooded areas and dense evergreen huckleberry (*Vaccinium ovatum*) and salal (*Gaultheria shallon*) on dry sites. Non-forest consisted of open sand and estuaries (Christy et al. 1998). Year-round temperatures were mild with mean minimum and maximum temperatures in July of 10.1°C and 20.3°C, and in January of 3.2°C and 10.2°C. Mean annual precipitation was 177 cm, mostly occurring as rain in November–March (Western Regional Climate Center 2016). We sampled martens between October 2009 and June 2013 in Lassen and late October 2015 through January 2016 in coastal Oregon.

Capture and handling.—We captured and processed martens using methods approved by Oregon State University and the USDA Forest Service's Institute for Animal Care and Use Committee (OSU: 3944, 4367; USFS: 2015-002), California Department of Fish and Wildlife Memorandum of Understanding with a Scientific Collecting Permit (803099-01), and Oregon Department of Fish and Wildlife Scientific Take Permit (119-15). We used capture techniques that minimized spread of diseases (Gabriel et al. 2012) and followed guidelines of the American Society of Mammalogists (Sikes et al. 2016). We trapped martens in Tomahawk live traps (105 and 106 models; Tomahawk Live Traps, Hazelhurst, Wisconsin) that we modified by attaching a custom-built wooden cubby. We used injectable anesthetics to immobilize captured martens (details in Mortenson and Moriarty 2015).

Telemetry data collection.—We collected 2 spatial data sets on the same individuals: 1) weekly or bi-weekly VHF telemetry locations used to create annual home range estimations using a minimum of 8 months of weekly location data, and 2) fine-scale movement data consisting of GPS locations collected over a short deployment lasting from a few days to 5 weeks. We fitted VHF or GPS collars to each adult marten suspected to be > 2 years old (verified via cementum annuli analysis—Bodkin et al. 1997) and presumed adult behaviors would be most representative of population-level socio-spatial organization. When using VHF telemetry, we located each individual weekly or bi-weekly using telemetry triangulations and by homing to locations where a marten was resting. We estimated accuracy of VHF locations using Location of a Signal (Ecological Software Solutions LLC, Hegymagas, Hungary) and discarded points with *x*- or *y*-variance > 400 m. The VHF data were used to estimate a range distribution, or the expected annual home ranges (Fleming et al. 2015).

We replaced the VHF collar with a GPS collar (41–44 g Quantum 4000 Micro-Mini; Telemetry Solutions, Concord, California or 27 g G10; Advanced Telemetry Systems, Isanti, Minnesota) up to once per season per individual, focusing on individuals > 650 g. GPS collars were programmed to collect location data every 5 min (G10) or once every 5 min only when the marten was active (Quantum 4000 with accelerometer). The GPS collars estimated location data (movement) for up to 5 weeks but battery life was typically limited to < 2 weeks (Moriarty and Epps 2015). We replaced the GPS collar with a VHF collar within 6 weeks of initial deployment and replaced VHF with GPS collars opportunistically year-round except 4 weeks before and 12 weeks after denning (i.e., no captures). We restricted our analysis to GPS locations with predicted error < 30 m (Moriarty and Epps 2015) and to periods where the GPS collar collected data for > 72 h up until the GPS collar battery died. Our 3-D fix success rates were 66 ± 12% and 58 ± 18% (mean ± *SD*) in Lassen and coastal Oregon, respectively, using Quantum 4000 collars, and 14 ± 6% in coastal Oregon with G10 collars. G10 collars collected data longer and while the animal was not moving and therefore could have been in cavities or underground, making fixes improbable. Because GPS data were collected over a short period of time, we estimated an occurrence distribution, or the spatial area used during a short period (Fleming et al. 2015).

Space use and overlap.—We used 2 representations of space use by martens: 1) 3-dimensional utilization distributions (UDs), which estimated the intensity of space use, which we used to estimate site fidelity and spatial overlap of neighboring martens of the same (intrasexual) and opposite (intersexual) sex, and 2) a 2-dimensional boundary estimate encompassing locations of martens (100% minimum convex polygon, MCP) for which we estimated extent of space use (area) as a function of time. Although the use of MCPs has been criticized (Laver and Kelly 2008), we used MCPs to describe the hourly increase in area as martens moved through their territories specifically because that method is sensitive to additional locations (Millspaugh and Marzluff 2001). To minimize the influence of potentially anomalous points on MCPs, we eliminated < 1% of outlying locations from each spatial data set (Harris et al. 1990). Distributions of locations for individual martens in both study areas were relatively convex, and no territories were broken up by large discontinuities in forest cover such as lakes. Therefore, MCPs appeared appropriate for our data and our need for precise exterior borders to track changes in space use accurately over time (Fieberg and Borger 2012). To test the difference between short- and long-term area used and fidelity between seasons, we compared areas estimated from movement (GPS) data to annual home range area (via VHF) and between seasons from areas created from GPS movement data using paired *t*-tests, whereby the

pairing was a comparison of individual martens or seasons for individuals with at least 2 seasons of data respectively. We reported area estimates from GPS movement data by sex, season, and study area.

We used UDs to describe: 1) uncertainty in animal location using long-term independently collected VHF location data (range distribution, 90% fixed kernel density estimation using likelihood cross validation—Horne and Garton 2006; Fleming et al. 2015), and 2) uncertainty in animal location between consecutive locations using Brownian motion (occurrence distribution, Brownian bridge movement model—Nielson et al. 2013). We were primarily interested in how well movement data from short-term GPS deployments represented long-term space use by martens. Occurrence and range distributions estimate uncertainty arising from different processes (long-term spatial requirements versus movement—Fleming et al. 2015), but because martens may move frequently within familiar areas and adult martens may have high site fidelity, we anticipated convergence between the 2 processes. For each animal, we constructed 1 range distribution using VHF location data and 1 occurrence distribution for each GPS sampling occasion (GPS deployment). To assess long-term space use and site fidelity, we compared spatial overlap of range distribution and occurrence distribution, as well as the occurrence distributions estimated for GPS deployments of the same individual in different seasons. We compared occurrence distributions for neighboring martens to evaluate intersexual and intrasexual overlap. We used the UD overlap for all spatial overlap comparisons. The utilization distribution overlap index (UDOI) estimated volume of spatial overlap between 2 UDs:

$$\mathrm{UDOI} = A_{i,j}\left(\iint \mathrm{UD}_i(x,y)\mathrm{UD}_i(x,y)\right)dxdy \qquad (1)$$

where UDOI was the sum of the product of the UD pair for all x, y locations where i and j represent 2 estimated ranges (e.g., estimated annual home range and territory from short-term GPS data from the same marten, estimated territories of neighboring martens—Fieberg and Kochanny 2005). The result was an index of overlap, ranging from zero (0) to near complete overlap (1), with occasional values > 1 when 2 non-uniformly distributed UDs have an unusually high degree of overlap.

Area-asymptote analysis.—We used incremental analysis (Kernohan et al. 2001) to calculate time to the maximum GPS deployment area, or the occurrence distribution (e.g., Fig. 1), and a mixed-effect model to estimate the cumulative territory occupied by an individual marten i up to hour h where the true size of the territory is unknown. The latent process for the marten's territorial area was described using a cumulative gamma distribution,

$$p_{i,j} = \int_0^{h(i,j)} f\left(\frac{\mu_i}{\beta_{h(j)}}, \beta_{h(j)}; x\right)dx$$

where $p_{i,j}$ is the cumulative proportion of the total area occupied; $f\left(\frac{\mu_i}{\beta_{h(j)}}, \beta_{h(j)}; x\right)$ is the gamma probability density function; μ_i is the expected number of hours it takes for the ith marten to occupy a portion of the territory (e.g., the mean, 50%); and $\beta_{h(j)}$ is the scale parameter for the gamma distribution during hour h. Because observations for the number of hours following GPS deployments were not consecutive within an individual, the variable $h(i, j)$ maps the jth observation for individual ith to the corresponding hours following GPS deployment.

The parameters of the gamma distribution (μ_i and $\beta_{h(j)}$) are random effects described by probability distributions defined

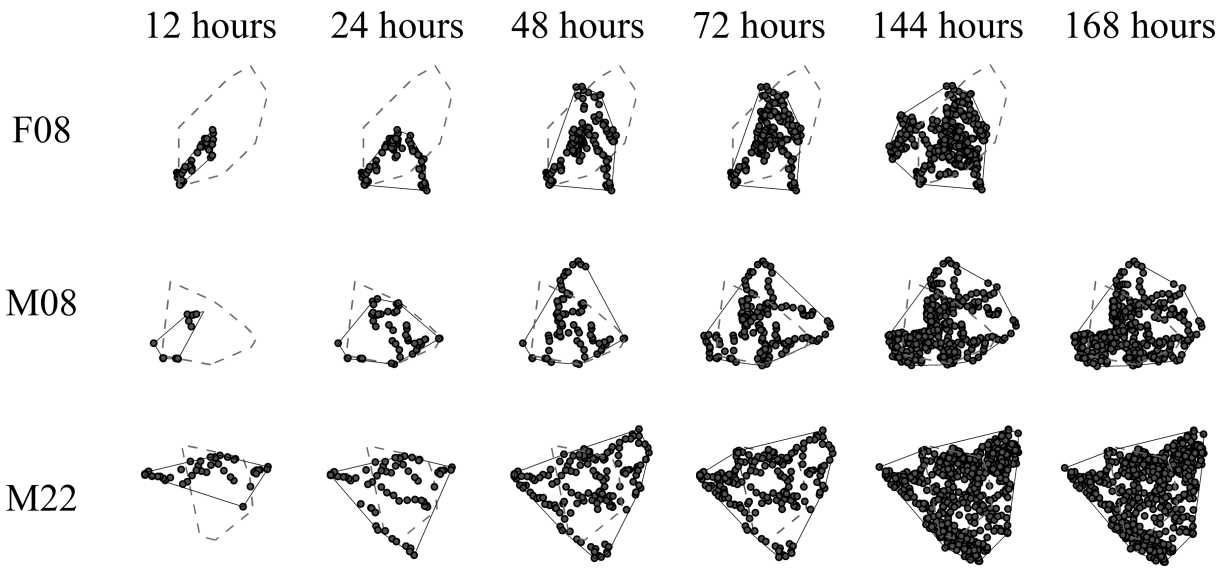

Fig. 1.—Representative spatial location data showing accumulation of area covered over time (12–168 h) for 3 Pacific martens (*Martes caurina*, males M22 and M08, female F08) on the Lassen National Forest, California (March 2010 to April 2013). Dots represent spatial locations collected at 5-min intervals using GPS collars. Dashed outlines represent annual ranges estimated from ground-based, year-round VHF locations (from top to bottom, n = 26, 69, 21). Solid lines represent cumulative GPS range after 12, 24, 48, 72, 144, and 168 h.

by set of additional parameters known as hyper-parameters; these hyper-parameters describe the distribution of the individual marten's characteristics within the population of martens. We assumed the parameter describing the hour at which the proportion (e.g., 50%) of the estimated occupied area was log-normally distributed with global population means of μ and *SD* of σ_μ,

$$\log(\mu_i) \sim N[\log(\mu), \sigma_\mu]$$

The scale parameter, $\beta_{h(j)}$, is characterized by a population mean β and log-normally distributed deviates (ϵ_h) for each hour with a mean of zero and *SD* of σ_β,

$$\beta_{h(j)} = \beta * \exp(\epsilon_h)$$

$$\epsilon_h \sim N(0, \sigma_\beta)$$

The estimated occupied area of the individual martens (A_i) is log-normally distributed with mean $\log(A)$ and *SD* of σ_A,

$$A_{i,j} = A_i p_{i,j}$$

$$\log(A_i) \sim (\log(A), \sigma_A)$$

The error between the estimated area from MCP for *i*th marten up the *h*th hour based on the *j*th observation, $X_{i,j}$, and the territory based on the asymptotic function, $A_{i,j}$, is normally distributed with a *SD* of σ_x,

$$X_{i,j} \sim N(A_{i,j}, \sigma_x)$$

The parameters of the model were estimated by maximizing marginal likelihood of the fixed and random effects given the data using a nonlinear optimization routines (Template Model Builder—Kristensen et al. 2016; equation 2),

$$L[\Theta, \tau | D] = \int_\epsilon \Pr(D|\Theta, \epsilon) \Pr(\epsilon|\tau) d\epsilon \quad (2)$$

where Θ is a vector of fixed effects (μ, β, A, σ_x); τ is a vector of random effect (μ_i, A_i, ϵ_h); *D* is the data (Thorson and Minto 2015); $\Pr(D|\Theta, \epsilon)$ is the likelihood of the data given the parameters and random effects; and $\Pr(\epsilon|\tau)$ is the probability of the random effect given the hyper-parameters τ ($\sigma_\mu, \sigma_\beta, \sigma_A$).

Since the gamma distribution describing the accumulation of occupied area as a function of time is a probability distribution, we calculated the probability that a marten will have occupied a given fraction (*s*) of its territory up to any hour based on the parameters (μ and β). For instance, the probability that a marten had occupied up to 75% of its territory was

$$P(X < 0.75) = \int_0^{x=h} f(x; \mu, \beta) dx \quad (3)$$

The benefit of this modeling approach is that the accumulation curve for each marten could be compared with a simpler 2-parameter model estimation without the assumption that a marten had reached a full territory. So, despite differences in GPS success and time within a deployment, this strategy could inform both overall model fit as well as estimate the time for an average marten to move around the perimeter of its territory. This approach therefore differs from models based from short-term observations assuming the animal's movements would be repeated within the estimated territory—and not expand beyond the observed boundary—following data collection (e.g., Potts et al. 2013).

Results

We sampled 22 individual martens using VHF collars for 19.9 ± 8.7 months on the Lassen ($\bar{X}$ ± *SD*, range 8–41 months, locations $\bar{X}$ = 39.3, range 21–91) and 11 martens for 2.5 ± 1.0 months in coastal Oregon. We deployed GPS collars on 19 adult martens in Lassen (5 females, 14 males) 40 times (1–3 GPS collar deployments per individual), and once per individual for 6 adult martens in coastal Oregon (3 females, 3 males). Sample sizes differed for each analysis due to a high failure rate of GPS collars (Moriarty and Epps 2015), low annual survival (0.63—Moriarty 2014), and differences in study periods between Lassen and coastal Oregon. Successful GPS collar deployments on Lassen (> 72 h; 7 female and 20 male occasions) collected a mean of 285.1 ± 30.1 ($\bar{X}$ ± *SD*) locations during 138.6 ± 7.04 h, and in coastal Oregon collected a mean of 500 ± 180.6 locations over 242.3 ± 99.1 h (3 females, 3 males).

In Lassen, the sizes of annual home ranges, or the range distribution estimated via VHF telemetry, and the occurrence distribution estimated via GPS telemetry were indistinguishable for females (n = 4 females, n = 6 GPS deployments; paired *t*-test, t_5 = 0.46, P = 0.66; mean of differences = 0.27; 95% confidence interval [95% *CI*]: −1.22 to 1.76 km^2) and for males (n = 5 males, n = 9 GPS deployments; paired *t*-test, t_8 = 1.42, P = 0.19; mean of differences = 1.74; 95% *CI* = −1.07 to 4.54 km^2). Spatial overlap for individuals with occurrence distributions in both seasons was high (UDOI = 0.99 ± 0.13 [$\bar{X}$ ± *SD*]). Thus, both area and the degree of overlap in space use supported the prediction that territories estimated using short-term movement data were indistinguishable from annual home range estimates (Fig. 1). We did not evaluate this metric in coastal Oregon due to the short period of VHF data collection.

Occurrence distributions for individuals were stable between seasons: we observed spatial overlap in Lassen of 0.86 ± 0.18 (females = 2, males = 5). We observed very low intrasexual overlap of neighboring martens tracked within the same season (e.g., Fig. 2; UDOI males = 0.02 ± 0.01, n = 13, females = 0.001 ± 0.001, n = 4) and coastal Oregon (females = 0.04, n = 2), suggesting exclusive territories among same-sex adults. Intersexual overlap was moderate (0.63 ± 0.18) using 4 male:female pairs in Lassen, providing evidence of tolerance between sexes. Although we did not attempt quantification, we also observed that martens appeared to reuse the same movement paths frequently within their ranges. We observed movements of different individuals that were sometimes linked closely in time (e.g., Fig. 3a) or space, despite differences in season (e.g., Fig. 3b).

Territories of males were significantly larger than those of females in both study areas (Table 1). In Lassen, territories of females in winter were generally > 4 times larger (4.02 ± 0.66 km^2, n = 4) than in coastal Oregon (0.84 ± 0.05 km^2, n = 3; Table 1). Similarly, territories of males in winter in Lassen were more than twice as large (8.22 ± 2.41 km^2, n = 10) as those in coastal Oregon (3.06 ± 1.28 km^2, n = 4; Table 1). No data were available for summer in coastal Oregon. In Lassen, sizes of territories with GPS deployments paired on the same individuals during both seasons were variable but slightly larger in the winter (t_6 = 2.19, P = 0.07, mean of differences = 2.57 km^2, 95% CI = –0.27 to 4.76; Table 1).

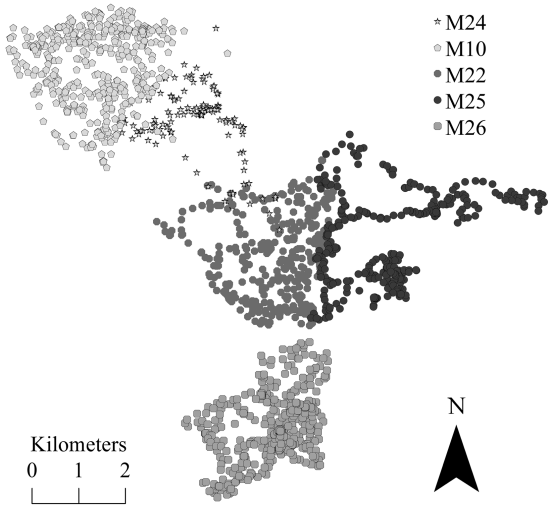

Fig. 2.—An example of intrasexual territoriality shown by 5 adult male Pacific martens (*Martes caurina*) followed using GPS telemetry on the Lassen National Forest, California. Data are for 18 February to 13 March 2012 except for M10, which was from 27 November to 3 December 2011. All locations have expected accuracy < 28 m (Moriarty and Epps 2015).

From the territorial asymptote model, using GPS data, the time required for individual martens to occupy 95% of their predicted territories ranged from 54.6 h (95% CI = 47.6–61.5) for a coastal male during winter (M02) to 273.6 h (95% CI = 273.8–348.8) for a Lassen male during winter (M25; Fig. 4). The model predicted observed movements relatively accurately (Fig. 4, gray line). Estimated cumulative territory occupied by the martens over time did not differ for groups based on sex, season, or location, except that females in Lassen during winter consistently had smaller territories than predicted by the model (Fig. 4). Across all martens, mean time to occupy 50%, 75%, and 95% of an individual's territory was 34.7 (95% CI = 28.7–40.7), 59.3 (95% CI = 48.9–69.6), and 110.9 (95% CI = 91.3–130.4) h, respectively (Fig. 5). Thus, our model predicted that martens on average moved over 95% of their territory within 4.6 days, although time to this threshold varied from 2 to 14 days across individuals (Fig. 4).

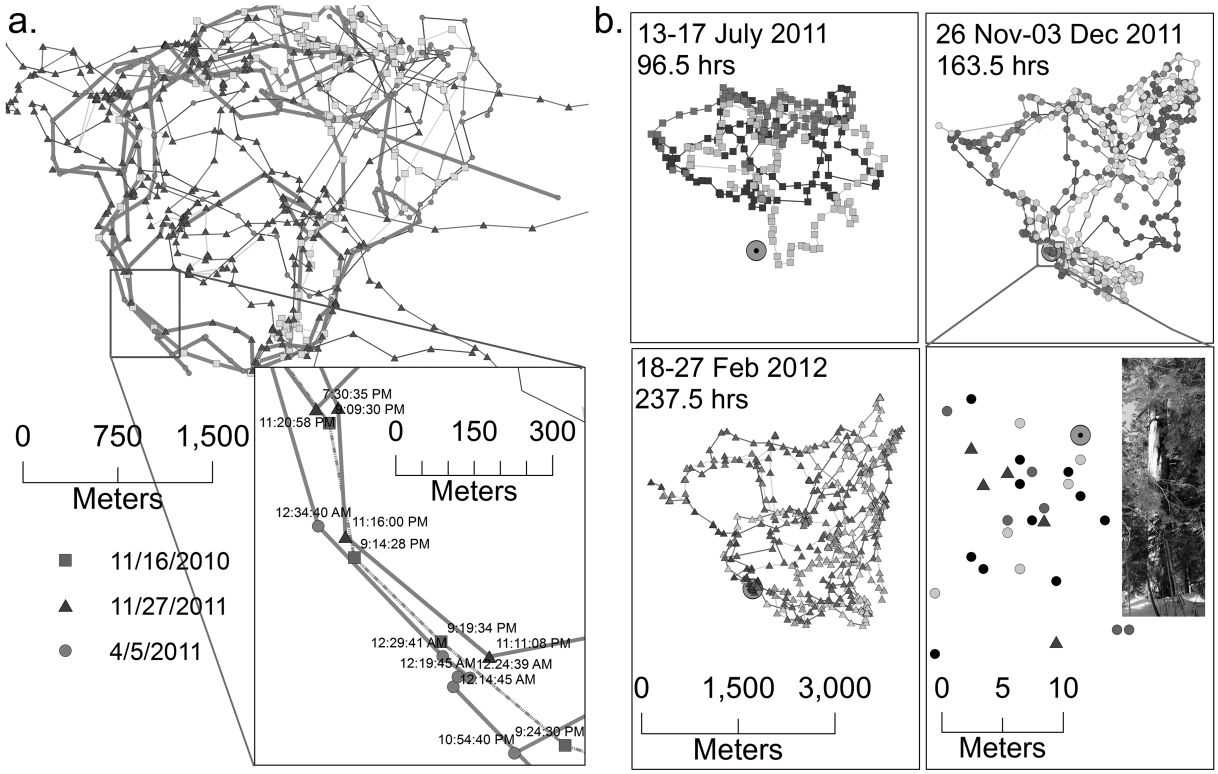

Fig. 3.—Two examples of suspected route reuse within territories by adult Pacific martens (*Martes caurina*) collected using GPS telemetry on the Lassen National Forest, California. (a) Male marten M10 appeared to traverse the same route (see inset with locations 30–64 m apart) at night on 3 occasions separated by 4–17 months (November 2010, April 2011, November 2011). (b) Male marten M22 frequented certain areas of the home range, where multiple routes were within 30 m of a prior occasion and locations were verified within 10 m on 4 occasions at a resting structure (a snag represented spatially as a circle with dot). Shaded dots and triangles represent separate occasions (days).

Table 1.—Mean territory size (km^2 for minimum convex polygons, 95% *CI* in parentheses) of Pacific marten (*Martes caurina*) in 2 study areas (Lassen, coastal Oregon) estimated using location data collected from short-term deployments of GPS collars (< 5 weeks). Summer = June–October; winter = November–May. We collected data from 19 martens at Lassen (n = 5 females, 14 males total; 3 females, 11 males in summer; 4 females, 8 males in winter) for a total of 26 GPS deployments. We collected data from 6 martens in coastal Oregon during winter (n = 3 females, 3 males).

Comparison	Females			Males		
	Lassen		Coastal Oregon	Lassen		Coastal Oregon
	Summer	Winter	Winter	Summer	Winter	Winter
Observed ranges	2.21 (1.93–2.50)	4.00 (3.36–4.63)	0.84 (0.78–0.90)	5.81 (4.20–7.44)	8.22 (6.55–9.89)	3.06 (1.81–4.31)
Modeled ranges	2.46 (2.33–2.59)	5.45 (5.19–5.71)	0.62 (0.55–0.67)	5.06 (4.91–5.20)	9.27 (8.85–9.69)	2.26 (2.17–2.34)

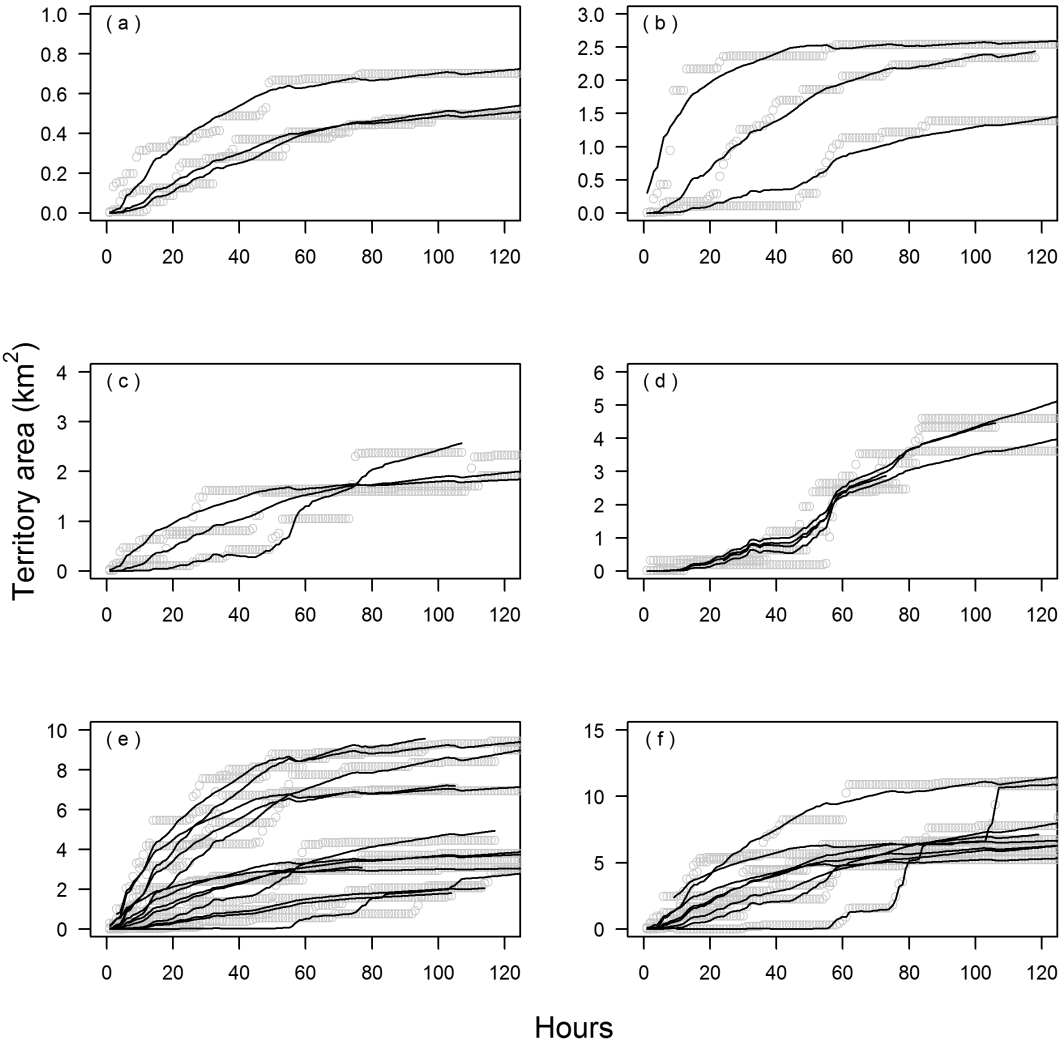

Fig. 4.—Relationship between time and territorial occupancy for 25 Pacific martens (*Martes caurina*) using high-resolution location data collected with GPS collars on the Lassen National Forest, California (n = 19, March 2010 to April 2013) and coastal Oregon (n = 7, October 2015 to January 2016). Gray dots represent the minimum convex polygon area estimate as a function of hours of data collection (x-axis) and area (y-axis). The black line represents the average accumulation curve scaled to the estimated territory size for each marten. Martens are grouped by sex, location, and season: coastal females during winter (a), coastal males during winter (b), Lassen females during summer (c), Lassen females during winter (d), Lassen males during summer (e), and Lassen males during winter (f).

Territorial areas predicted from the model ranged from 0.53 km^2 (95% *CI* = 0.43–0.63) for female F01 along the coast during the winter to 40.7 km^2 (95% *CI* = 27.2–52.8) for male M25 at Lassen during the winter. With the exception of M25, the *CI*s around the individual estimates of territory size were small; the reason for M25's large predicted range was unclear (Table 1; Figs. 4 and 5). Our modeled territory sizes differed based on sex, season, and location (Table 1). Across study areas, territories predicted for males were roughly twice as large as territories predicted for females (Table 1). Territorial areas of males did not differ between summer and winter when removing the modeled outlier (M25; 5.06 km^2,

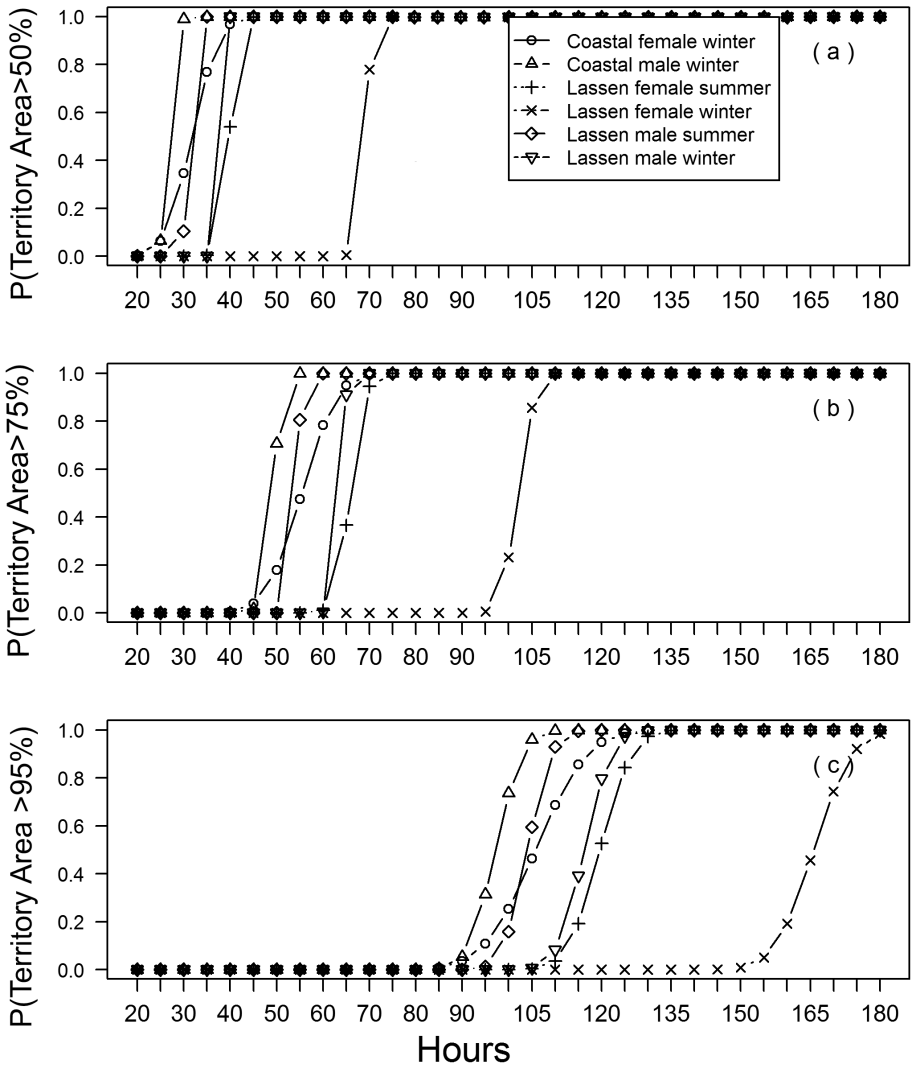

Fig. 5.—Distributions of the uncertainty in the hours following GPS deployment and the fraction (a: 50%, b: 75%, c: 95%) of territory occupied for 25 Pacific martens (*Martes caurina*) with high-resolution location data collected with GPS collars in Lassen National Forest, California ($n = 19$, March 2010 to April 2013) and coastal Oregon ($n = 6$, October 2015 to January 2016). Our modeled calculations were generally consistent between study areas, sexes, or seasons (see legend), but we observed a slightly longer modeled time period for female martens in Lassen during winter ("x").

95% *CI* = 4.91–5.20 versus 5.83 km^2, 95% *CI* = 5.76–5.91, respectively).

Discussion

Pacific martens in both a coastal and a montane study area exhibited frequent and comprehensive territorial movements. On average, an individual's movements defined 95% of its territory within 4.6 days, and this time period was consistent among sexes, study areas, and seasons. Thus, our observed data were consistent with the hypothesis that martens engage in frequent movements that maintain the boundary of their territory. Location and size of annual territories inferred using long-term VHF telemetry data closely matched areas used estimated from short-term GPS movement data for the same individuals, and site fidelity was high among seasons. As predicted, martens also exhibited little spatial overlap among neighboring same-sex individuals (Fig. 2) and tolerated moderate overlap between sexes. Thus, we conclude that short-term movement data (2–14 days) sufficed to estimate long-term marten territories in these 2 very different study areas (coastal Oregon and montane Lassen), and that such high-resolution data offer new opportunities to understand the socio-spatial organization of these populations.

Marten movements were the expression of multiple behaviors that maximize fitness, including foraging and scent marking, and reflect territoriality. If movement rates were influenced by scent marking, then movement rates should in part be a function of the time period over which scent is effective (e.g., 3–10 days in other species—Balharry 1993; Jedrzejewski et al. 2001; Zalewski et al. 2004; Potts et al. 2013). Pacific martens in our study traversed the perimeters of their territories and 95% of the areas in an average of 4.6 days, similar to pine martens that traversed 86 ± 9% of their territories in 5 days in Scotland (Balharry 1993) and 3–10 days in Poland (Zalewski et al. 2004). We hypothesize that under most conditions, ~5 days

may be the maximum amount of time for which a scent mark from a marten communicates to other martens that the territory is occupied. Other species with similar behaviors may be good candidates for evaluating whether movements over short periods of time are sufficient to identify territory boundaries. The unpredictable nature of foraging success (i.e., prey availability, capture success) has been predicted to increase both movement rates and territoriality in other carnivore species (wolverines [*Gulo gulo*]—Mattisson et al. 2016; lynx [*Lynx lynx*]—Herfindal et al. 2005; wolves [*Canis lupus*]—Jedrzejewski et al. 2001). Thus, we predict that species that rely on mobile and uncommon prey are most likely to exhibit territorial movements similar to those of Pacific martens. For instance, wolves moved through > 70% of the area of their territories in Poland every 8 days on average, with increased frequency of exterior boundary movements during the breeding season (Jedrzejewski et al. 2001). Foxes in Bristol, England, moved along the exteriors of their territories in 5 days, increasing their movements to every 3 days following a population perturbation due to disease (Potts et al. 2013). Similarly, wolverines in Wyoming cover > 75% of their range in < 32 days (Inman et al. 2012). We predict many territorial carnivores will also move along the exterior border with predictable frequency.

Although we did not explore the patterns of movements within the territories, the high degree of spatial overlap between territories calculated using short-term movement data and territories calculated using long-term annual data suggested that martens frequented most portions of their territory (Fig. 3). This pattern also led to high territorial fidelity between seasons, similar to that described for pine martens (Zalewski and Jędrzejewski 2006) and American martens (*Martes americana*—Phillips et al. 1998). We suspect that martens reuse familiar travel routes within their territory (Fig. 3), and such reuse may confer fitness advantages such as reduced risk of predation due to familiarity with cover or shelter, increased food acquisition due to familiarity with microhabitats used by prey, and—if overlapping territories include travel routes used by both sexes—increased mating opportunities. We also observed extremely low intrasexual overlap (Fig. 2), which may indicate defense of limiting resources.

Precisely monitoring territory size and use over short time periods could offer new insights regarding when and how populations may be affected by changes in their environments. For instance, martens are particularly susceptible to habitat loss and fragmentation, and populations can become locally extirpated when as little as 25–33% of the forest cover in a landscape is removed by timber harvest (Hargis et al. 1999; Potvin et al. 2000; Fuller 2006). Because we documented here that annual territories of martens can be described with, on average, < 1 week of data, repeated measurements of territory boundaries and individual movement patterns offer the possibility of using a species-centered approach to understand responses to habitat loss and fragmentation, as recommended by Betts et al. (2014). For instance, measuring territorial movements during habitat loss (e.g., timber harvest) or through stochastic environmental variation could provide an opportunity to test hypotheses as to why populations are limited following disturbance.

Advances in techniques for home range estimation using short duration but numerous telemetry locations (Lyons et al. 2013; Fleming et al. 2015) provide the capacity to reimagine the study of territorial behavior. For carnivores that scent mark the perimeters of territories, even short-term GPS deployments can produce data that are highly informative, potentially increasing sample size and sampling efficiency, and allowing a deeper understanding of socio-spatial structuring. GPS collars have great potential for obtaining vast quantities of location data uninhibited by weather or time of day, but also can have high failure rates—especially for collars < 60 g (e.g., Cypher et al. 2014; Moriarty and Epps 2015)—and can suffer from missing or imprecise data in areas with high vegetation or topographical cover (Cagnacci et al. 2010).

We envision that collecting GPS location data during biologically relevant time periods (> 4.5 days in our study) to estimate territories will improve the quality of studies of population dynamics and social systems, because many dynamics of socio-spatial organization may be obscured when estimating home range or territory over seasonal or annual time frames. Moreover, changes in the social environment that occur with births, deaths, and changes in habitat may alter territory shape and social structure in a short period of time; thus, observation periods that encompass such changes may produce uninformative representations of social structure. Comparing movement data over time for additional species, ideally where spatial and temporal variation in resource availability is known, will help determine the generality of the results of this study.

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