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Weasels *Mustela* spp. are specialized, small predators which demonstrate pronounced differences in size and social status according to sex and age, and these differences may manifest in spatial patterns including home range size and habitat selection. In forested North America, favored prey (voles; *Microtus* spp. and *Myodes* spp.) of short-tailed weasels *Mustela erminea* often reach high abundances in early stage forest, but availability of that cover type is limited where intensive plantation forestry occurs. We estimated home range size, including home range core area and arrangement, habitat selection, wet season rest site reuse and movements for 25 (18 M: 7 F) short-tailed weasels *Mustela erminea* that we radio-collared in managed plantation forests in western Oregon, USA in 2012–2013. Average fixed kernel 90% home range size was 51.3 hectares for males (95% confidence interval = 30.8–71.7 ha) and 8.6 hectares for females (95% confidence interval = 6.41–10.79 ha). Juvenile males had larger core areas than adult males, and all females had similar core areas. Core areas for all individuals were negatively correlated with % early stage forest cover. Females strongly selected early stage forest cover at both study area and home range scales, and males were less selective of particular cover types. Home ranges of observed males did not overlap, but partly overlapped the home ranges of females. Short-tailed weasels reused the same rest site in 43% ± 4 (mean ± SE) of cases observed during the wet season (n = 10 individuals, 292 rest sites). We conclude that space use by short-tailed weasels in western Oregon is influenced by sex, age, and cover type, especially availability of early stage forest, in managed conifer forests.

Short-tailed weasels *Mustela erminea* are small, specialist predators of rodents and widely distributed in the northern hemisphere. Their morphological (long, narrow body profile, short fur; Brown and Lasiewski 1972, King and Powell 2007), biological (delayed implantation; Ternovsky 1983), and behavioral (erratic movement patterns, occupancy of prey nests; Fitzgerald 1977, Powell 1978) adaptations represent tradeoffs and adaptations to an uncertain environment (fluctuating prey populations, variable temperatures, predators; King and Powell 2007). Sexual dimorphism may further represent a sex-specific adaptation which limits intersexual competition for food (Brown and Lasiewski 1972), or as a response to sex-specific reproductive demands (Erlinge 1979). Females are smaller than males; small body size in females is hypothesized to be an adaptation to the rigors of raising their young alone, limiting female energetic needs, while facilitating access to the burrows of the most abundant local prey (Erlinge 1979, Simms 1979a). In contrast, males are hypothesized to prioritize both foraging success

and access to female mates, and larger bodied males may be dominant over smaller males, including juveniles (Erlinge and Sandell 1986). Tradeoffs between sex-specific resource priorities are hypothesized to manifest in diet and space use differences between males and females (Erlinge 1979).

Sex-specific habitat selection and home range size are likely to be strongly influenced by prey type and distribution, and predator avoidance. Short-tailed weasels are dependent on prey for food and refuge (Fitzgerald 1977), and inhabit areas with dense ground cover, which facilitates prey capture and avoidance of predators (Simms 1979a, Koivisto et al. 2016). The location and size of the home range, the area in which an individual can find sufficient resources to survive and reproduce (Burt 1943), strongly differs by sex (Table 1). For example, female short-tailed weasels consistently have smaller home ranges and select vegetation cover types with high prey abundance (Hellstedt and Henttonen 2006), often in open grassland or early seral stage forest (Simms 1979b, Sullivan and Sullivan 1980, Lisgo 1999). Compared to females, male short-tailed weasels tend to use a broader range of prey types and prey sizes (Raymond et al. 1990, Vaudry et al. 1990, Lisgo 1999, Edwards and Forbes 2003), and to be less selective of particular cover types (Lisgo 1999, Hellstedt and Henttonen 2006). Exclusive use areas may limit intrasexual resource competition but require

Table 1. Reported home range sizes of male and female *Mustela erminea* and *Mustela frenata* in North America, arranged in order of increasing latitude (mean ± 1 SD).

			Males			Females		
Reference	Location (latitude)	Estimator[a]	Mass (g)	Area (ha)	n	Mass (g)	Area (ha)	n
Mustela erminea								
Simms 1979b	Ontario, CAN (43°50′)	CMR	100.7[c]	21.3 ± 3.5	8	57.1[c]	8.3 ± 3.5	4
Linnell 2014	Oregon, USA (44°93′)	90% FK	74 ± 7.3	51.3 ± 14.3	18	46 ± 4.6	8.6 ± 0.6	7
		100% MCP	74 ± 7.3	42.6 ± 7.6	18	46 ± 4.6	6.0 ± 6.3	7
Raymond and Robitaille 1995	Quebec, CAN (45°22′)	CMR	110.3[c]	19.8 ± 24.7	11	59[c]	4.8 ± 3.5	12
St-Pierre et al. 2006	Quebec, CAN (47°81′)	100% MCP	129 ± 26	126.9 ± 109.2	15	77[c]	68.9[c]	1
Lisgo 1999	Alberta, CAN (54°58′)	95% FK	193 ± 32	148 ± 38	4	87 ± 12	80 ± 12	4
Mustela frenata								
Richter 2005	Indiana, USA (38°02′)	95% FK	n/r	49.6 ± 26.5	4	n/r	21.6 ± 9.6	4
Hajduk 2008	Indiana, USA (38°02′)	95% FK	n/r	28 ± 9	7	n/r	18.9	1
Gehring and Swihart 2004	Indiana, USA (40°23′)	95% AK	195 ± 8[b]	180.3 ± 60.3	7	111 ± 5	51.8 ± 8.1	4
St-Pierre et al. 2006	Quebec, CAN (47°81′)	100% MCP	209 ± 70	141.9 ± 127.2	14	146 ± 13	81.1 ± 70.4	6

[a]capture–mark–recapture method (CMR), fixed kernel (FK), adaptive kernel (AK), minimum convex polygon (MCP).
[b]adult males; juvenile males = 162 ± 9 g.
[c]only the mean was reported.

defense of part or all of a home range (territories, Burt 1943). Segregation into intrasexual territories is considered the null hypothesis in studies of larger mustelids (Powell 1979), but has not been evaluated for smaller mustelids.

For weasels, intrasexual territoriality may occur seasonally or not at all because of high adult mortality (Debrot and Mermod 1983, Linnell et al. 2017) and fluctuating prey resources (Erlinge 1983). When and where rodents are less numerous, and potentially during the breeding season (May–July in the Northern Hemisphere), short-tailed weasels may be less territorial as males roam more widely seeking prey and mates (Debrot and Mermod 1983, Erlinge and Sandell 1986). During the non-breeding season, adults (> 1 year old, age of sexual maturity in short-tailed weasels) may maintain territories and juveniles (< 1 year) may be non-territorial (Erlinge 1977, Erlinge and Sandell 1986). The polygynous or promiscuous mating system exhibited by weasels probably favors sex-biased dispersal whereby females settle in home ranges close to natal areas, and juvenile males disperse (Erlinge 1979, Greenwood 1980). Low annual survival (estimated to be 0.37 ± 0.28 [mean ± 1 SD] across seven studies in North America; Linnell et al. 2017) and high annual turn-over of resident adults defending territories (Erlinge 1983, Debrot 1984) may result in destabilization of a territorial system or potential opportunities for juveniles to settle close to natal areas.

Short-tailed weasels in the Pacific states of western North America are the smallest throughout that species' circum-boreal distribution (31–86.5 g), and overlap with the larger long-tailed weasel *Mustela frenata* (Verts and Carraway 1998). Although studies are limited in western North America, short-tailed weasels probably specialize on *Microtus* spp. *and Myodes* spp. voles which they pursue into the voles' nests, often converting those nests to meet their own thermal and resting requirements (Fitzgerald 1977). In the Pacific Northwest and elsewhere in forested North America, *Microtus* spp. voles, in particular, are most common in non-coniferous cover types, often the early stage of forest succession (early stage forest; Simms 1979b, Wilson and Carey 1996, Gomez and Anthony 1998), and short-tailed weasels are also in early stage forest (Simms 1979b,

Sullivan and Sullivan 1980, Hall and Kelson 1981, Wilson and Carey 1996, Gomez and Anthony 1998, Mowat and Poole 2005). Plant species diversity and temporal period of early stage forest, however, is often limited in managed forests due to rapid establishment of densely planted conifers and reduction of non-coniferous vegetation (Swanson et al. 2011). Systematic evaluations of space use by short-tailed weasels in managed forests or other North American cover types has been limited by difficulty in capturing and monitoring sufficient individuals, particularly given constraints on collar size and longevity due to the small size of this species (Table 1).

In this study, we estimate home range size and overlap, habitat selection, and movements of short-tailed weasels using radio-telemetry in conifer plantations of western Oregon. Our objectives were to evaluate the relative influence of early stage plantation forests (e.g. 5–15 years post-harvest), season, and sex and age classes on movements, rest site reuse rates, and location and size of home ranges of short-tailed weasels. We assessed spatial segregation of adult home ranges, predicting moderate-high intersexual overlap and low intrasexual overlap. We predicted juveniles would be non-territorial and would use large home ranges including cover types avoided by adults. Finally, we evaluated sex-specific philopatry, predicting that maximum distances moved by juvenile females would be shorter than those by juvenile males.

Study area

The study was conducted in June 2012–April 2013 on a 9.2 km² area of the 45.5 km² McDonald-Dunn Research Forest, 12 kms north of Corvallis, Benton County, Oregon. McDonald-Dunn Research Forest was managed by the Oregon State Univ. Dept of Forestry, and was located in the foothills of the Oregon Coast Ranges at the western edge of the Willamette Valley. Vegetation included a complex mosaic of early stage, mature and old conifer forests, recent clearcuts, riparian forest, oak woodlands, abandoned farm fields and actively cultivated farm fields. We classified six vegetation cover types based on forest stages (Table 2); forest

stage classifications were based on Gomez and Anthony (1998). In the central Oregon coast ranges (Lincoln, Benton counties), abundances of the most common small voles (*Microtus oregoni*, 19.3 ± 0.73 g, Verts and Carraway 1998) were estimated to be ~14 times lower 20–35 years post harvest compared to early stage (5–10 post harvest; Gomez and Anthony 1998).

Predominant silvicultural practices resulted in 5–15 hectare clearcuts that were replanted 1–2 years post harvest. Spraying of non-coniferous vegetation, dense replanting of conifers, and rapid conifer growth in clearcuts resulted in establishment of primarily conifers and wind-dispersed species such as grasses. Forest canopy closure primarily occurred at ~10–15 years post harvest. Conifer forest areas were dominated by Douglas-fir *Pseudotsuga menziesii* and riparian forests were dominated by hardwood trees. Terrain in the study area was moderately steep with numerous small streams. Elevation ranged from 100 to 553 m and average annual precipitation was 1030 mm (Western Regional Climate Center 2014). The majority of precipitation occurred as rain during fall, winter, and early spring (November–March, wet season) which mostly corresponded to the non-breeding season for short-tailed weasels.

Methods

Capture and handling

We trapped and radio-collared weasels each month from June 2012–March 2013. We modified Tomahawk no. 102 live traps to include a protective enclosure (cubby), flooring, waterproof cover (Linnell 2014), and placed traps at 50 m-intervals along 12 transects, each with 5–9 traps, distributed in all cover types. Transect length varied from 200–400 m due to differing feature lengths and access. We placed traps in sites with abundant ground cover such as slash piles, thick shrubs or dense grass (Lisgo et al. 2002). Additional traps were opportunistically placed at features along roads, including slash piles and stream crossings. To improve trapping success we monitored activity at traps between trapping sessions using sticky tracking paper and printer ink toner applied within the trap. We used lure as an attractant (Weasel Super All Call Lure, Asa Lenon) and inactivated the trap by wiring open the door. During trapping sessions, we removed the wire, and set the trapping pan to trigger with a single finger touch; each trap was baited with lure and a fresh dead lab mouse *Mus musculus*. We trapped bi-monthly during the study, activating up to 20 traps per trapping session such that all traps could be checked in < 2 h by one observer.

Traps were checked once per 24-h. Upon capture, the weasel was released into a 5-liter clear plastic handling bag and sedated with 2 ml of isoflurane (99.9%) soaked in a cotton ball and placed within a perforated 50 ml conical vial placed in the handling bag. Handling bag volume was then reduced to ~2 l by creasing and folding the top opening down. The weasel was monitored visually in the handling bag, and removed when sedated, typically about 2 min. Sedation was maintained by placing a 50 ml conical vial with 0.6 ml of isoflurane soaked in a cotton ball over the snout of the weasel for < 10 s as needed. Total handling time was typically < 7 min.

During handling, we determined the sex, age, weight and attached a 1-g (females) or 2-g (males, females) radio collar to each individual captured (model BD-2C, Holohil Systems, Carp, Ontario, Canada). The expected life span of radio collars was 6–11 weeks for two gram collars and 6–8 weeks for one gram collars. We categorized males as adults if they had descended testes or evidence of previously descended testes (King and Powell 2007). Surface area of the scrotum was visibly larger in males with regressed testes (adults) compared to males with testes that had not yet descended (juveniles). Females were classified as adults if they showed signs of previous breeding (obvious teat development) or juveniles if they did not.

Radio-tracking

Home ranges were calculated based on daily locations of radio-marked individuals. We relocated each radio-collared weasel once daily (4–7 times per week), and attempted to obtain locations at night by occasionally rotating the weekly sampling to a different six-hour observation block. We monitored the radio signal for 1–3 min and noted fluctuations in the signal indicating movement. If the

Table 2. Vegetation cover types on the McDonald-Dunn study area, Benton, County, Oregon, USA, adapted from Gomez and Anthony (1998).

Cover type	Mean canopy cover	Stand age (years)	Percent of study area	Description
Grass conifer	11%	5–15	29%	Early stage vegetation on regenerating clearcuts. Grasses dominate gaps between re-planted Douglas-fir (*Pseudotsuga menziesii*) trees.
Pole stage	86%	16–30	6%	Stem exclusion phase on clearcuts, as young Douglas-fir trees shade out grasses and competing shrubs.
Sawtimber	92%	31–109	46%	Closed canopy Douglas-fir plantations with some undergrowth, mostly ferns.
Mature	93%	110–332	7%	Closed canopy Douglas-fir. Natural canopy gaps, woody debris at forest floor due to windfall, regenerated after fire.
Riparian	85%	52–67	5%	Hardwood dominated (~70%) streamside habitat.
Field	21%	N/A	7%	Fields with some grazing or hay production. Dominated by grasses, shrubs, and blackberries. Localized high densities of subterranean tunnels created by pocket gophers (*Thomomys bottae*) and moles (*Scapanus* spp.).

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signal remained constant, we assumed the weasel was resting (inactive), and attempted to obtain a resting location by directly approaching the signal on foot until we were within ~5 m. Most rest site locations were obtained in the wet season. If the weasel was moving (active), one observer obtained ≥ 3 bearings, ≥ 20 degrees apart, in < 15 min. Most (82%) locations were collected within 30 m of the animal, therefore we estimated telemetry error as < 30 m.

Core area estimation, habitat selection and spatial overlap

We estimated home ranges and core areas for short-tailed weasels. Core areas are often estimated using an arbitrarily designated isopleth value applied across all individuals in a study (Vander Wal and Rodgers 2012). Core area estimates, however, can vary by individual, and represent the area of most intense use within the home range (Powell 2000). The core area isopleth is identified where isopleth volume increases faster than area (x–y spatial extent, Vander Wal and Rodgers 2012). Therefore, we used a unique core isopleth estimated for each individual as described below to define core areas for use in analyses. First, we estimated fixed kernel (FK) utilization distributions (UDs, Seaman and Powell 1996) using the plug-in method to select bandwidth (Beyer 2012, Horne and Garton 2006). We selected the direct plug-in method because cross validation methods, such as likelihood cross validation, appeared to over-smooth and fragment, especially areas of intense use (core areas). Second, we estimated home ranges at the 90% isopleth of the UD because the 95% isopleth appeared to over-estimate the home range (Börger et al. 2006). Third, to identify the core area within that home range, we fitted an exponential regression curve where percent area was estimated at 5% increments of the maximum home range (y-axis) and isopleth volume at 5% increments (x-axis). We selected the core isopleth as the 5% increment where slope was closest to equaling 1 (Vander Wal and Rodgers 2012). Although Börger et al. (2006) suggested that ten should be the minimum number of relocations for home range estimation if animals are sampled daily, we estimated home ranges for all animals with eight or more locations because of limited numbers of females. This allowed us to include two females with only eight locations; all other animals included had > 10 locations. To ensure that number of locations did not unduly influence our results, we 1) used a linear model to estimate the correlation between number of locations and core area, and 2) compared number of locations used to estimate core areas for males and females using a t-test. We also estimated home range size with the 100% minimum convex polygon method (MCP) to facilitate comparisons with previous studies (Table 1, King and Powell 2007). At the conclusion of the study, we attempted to retrieve radio-collars from radio-tracked individuals.

We used first return height distributions from an airborne LiDAR layer created in 2008 (Goerndt et al. 2010) to identify early stage vegetation with grass or sapling cover (< 1.0 m vegetation height). Our study began four years after the LiDAR data was collected, and within the study area no recent timber harvest had occurred. Consequently, our height strata represented recent clear-cuts with dense re-generation of grasses, small conifers, and some shrub species

(henceforth, early stage cover, < 1.0 m height), closed canopy plantations (forest cover, ≥ 1.0 m vegetation height, e.g. sawtimber, Table 2), and a gradient for our other vegetation classes (Table 2). Estimated tree height measurements from LiDAR were accurate to < 1.17 m, and individual stems were identified to within 2.31 m compared to ground plots (Edson and Wing 2011).

We used the six cover types (Table 2) to conduct weighted compositional analyses of habitat selection at the study area scale and home range scale (Johnson 1980). Weighted compositional analysis uses the UD volume within each cover type to calculate the proportional use of cover types by each individual and compares this to the proportion of available cover types within the study area or the home range. We defined the study area as the combined 99% FK isopleths for all weasel locations. To reduce type I error, we substituted 0.3% for all zero value cover types (Bingham and Brennan 2004).

To evaluate whether home range and core area were exclusively used, we estimated the home range and core area overlap of pairs of neighboring weasels tracked during the same month, including overlap between adults of the same sex, adults and juveniles, juveniles and juveniles, and females and males using the utilization distribution overlap index (UDOI, Fieberg et al. 2005). We attempted to capture neighboring individuals of both sexes and ages, but because we probably overlooked some individuals – particularly females which are more difficult to capture (King 1975, King and Powell 2007) – our estimates of overlap were probably biased low.

Home range model variables and model selection

We created three univariate models and one two-variable model to test hypotheses about the relative influence of SEX, AGE, and % forest cover (%FOREST_COVER) on core area size. We first examined residual plots of all variable combinations, identified collinear variables, and log-transformed estimates of core area (response variable) to normalize residuals. We used AICc model selection adjusted for small sample sizes to select best models (Burnham and Anderson 2002). To estimate beta coefficients for individual variables we used the top ranked model that contained that variable.

Movement and rest site reuse

We also evaluated movement and rest site use by season and group where each group represented a unique age class and sex combination, e.g. juvenile female. We estimated the mean and maximum daily distance, i.e. distance traveled in a 24-h period, that each radio-collared weasel moved during the period in which it was tracked, and compared this among sex and age groups using t-tests. We estimated a reuse index as the proportion of resting locations that occurred in a previously used resting location (Zalewski 1997). Because we expected rest site reuse to be sensitive to total number of resting locations and days tracked, we limited our analysis to animals with > 10 rest sites, tracked for > 10 days. We estimated rest site reuse during the wet season, but not the dry season due to limited data. For all comparisons, we used

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Welch's t-test because none of our comparisons had equal sample sizes or variances.

Results

Capture, handling and radio-tracking

We captured 33 short-tailed weasels (23 M, 10 F) 43 times during 947 trap nights in June 2012–March 2013 (4.5 captures/100 trap-nights): one died in a trap, one died during handling, one died within 24-h post release, one we released without collaring because it was too small to radio-collar (38 g female), and 25 were radio-collared long enough to estimate home ranges (Supplementary material Appendix 1). Mean mass of males and females was 73.6 ± 7.3 g (mean $\pm$ SE) and 46.0 ± 4.6 g, respectively. We tracked an average of 7.5 individuals per month (range: 3–13) and obtained an average of 36 locations per individual (range 4–146). Most observations (80%) were between 04:00–16:00 h PST. Seven individuals (6 M, 1 F) removed their collars after an average of 22 tracking days (range = 7–48 days), limiting our data from those individuals, including one large male (86.5 g) that slipped his collar on three different occasions.

Core area estimation, habitat selection and spatial overlap

Number of locations was similar between males and females ($t_{8.3} = 0.13$, $p = 0.90$), and number of locations was not correlated with core area ($r^2 < 0.001$). Mean core area isopleth was 0.5 ± 0.045 (mean $\pm$ SD; range 0.4–0.55). Core area was similar in juvenile females (2.40 ± 0.17 ha) and adult females (2.20 ± 0.52 ha) but differed for juvenile males (25.90 ± 6.60 ha) and adult males (9.35 ± 2.18 ha; Fig. 1, 2). Home range size between the dry and wet seasons did not differ ($t_{23} = 0.08$, $p = 0.94$) after accounting for sex. Female
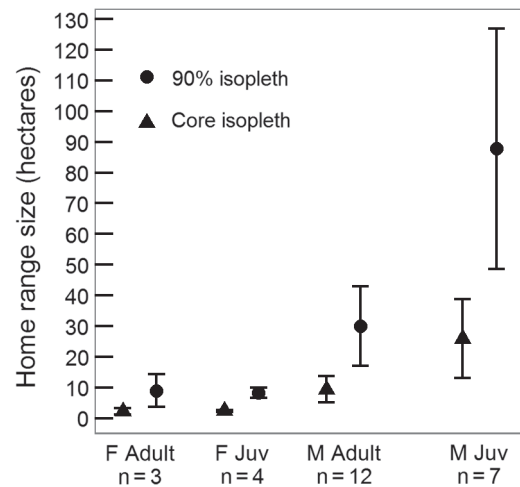

Figure 2. Short-tailed weasels home range sizes (triangles) and core areas (circles) for all sex and age classes (female (F); male (M)) in Corvallis, Oregon, USA, 2012–2013.

core areas were composed primarily of early stage cover (grass conifer, grass; $88\% \pm 1.3\%$), whereas male core areas were composed of lower and more variable proportions of early stage cover ($55\% \pm 6.7\%$). Females consistently selected cover types consisting of early stage cover types (grass conifer, field) at both the study area and home range scales, whereas males showed less obvious patterns at both scales (Table 3, Fig. 3). Both sexes avoided the sawtimber cover type (Table 2; trees 31 to 109 years old) at the home range scale.

Spatial overlap of home ranges was lowest amongst adults of the same sex; intrasexual overlap of core areas was particularly low. In contrast, intersexual spatial overlap was comparatively high but variable. The pattern of spatial overlap among juveniles was highly variable (Fig. 4).
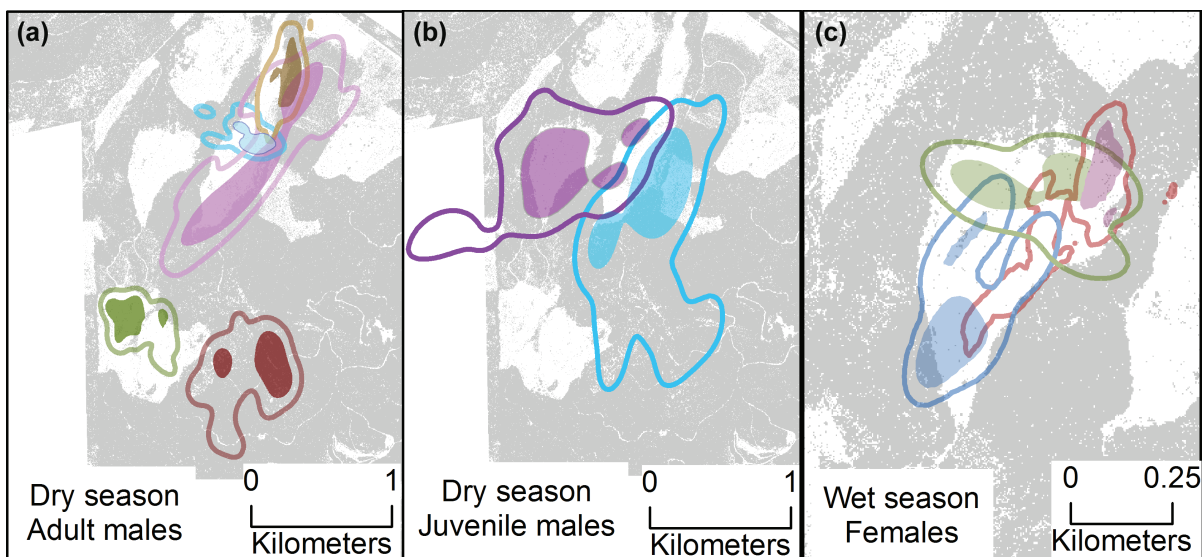

Figure 1. Examples of short-tailed weasel home ranges (90% fixed kernel; lines) and core areas (45% to 55% fixed kernels unique to individual; solid) in the dry season (June–October 2012) and the wet season (November 2012–March 2013) in western Oregon. Background shading represents conifer cover ≥ 1 m height (dark shade), and open cover types < 1 m height (no color; < 1 m height; grass conifer). Sample sizes in a) n = 5, b) n = 2, c) n = 2 adults (green; blue), and 1 juvenile (red).

Table 3. Results of weighted compositional analysis of habitat selection by short-tailed weasels (18 M, 7 F) on the McDonald-Dunn Research Forest, Benton County, OR, USA, June 2012–January 2013. Results are presented separately for analyses based on the study area and home range scales.

Selection	Cover type rankings
Study area scale	
all animals	grass conifer[1] > riparian[2] > sawtimber[3] > field[3] > pole stage[4] > mature[4]
males	riparian[1] > grass conifer[1] > sawtimber[2] > field[2] > pole stage[2] > mature[2]
females	grass conifer[1] > sawtimber[2] > field[2] > riparian[3] > mature[3] > pole stage[4]
Home range scale	
all animals	grass conifer[1] > field[1] > pole stage[1] > mature[1] > riparian[2] > sawtimber[2]
males	mature[1] > riparian[1] > pole stage[1] > grass conifer[1] > field[1] > sawtimber[2]
females	grass conifer[1] > field[1] > pole stage[2] > riparian[2] > mature[3] > sawtimber[3]

Numbers represent significant differences between cover types ($\alpha < 0.05$, two sample t-test). The difference between cover types with the same number is non-significant.

Home range model variables and model selection

Sex and age were the primary influences on core area (Table 4). Adult males weighed 11.8 grams (mean; 95% confidence interval = 7.7, 15.9) more than juvenile males ($t_{19} = 6.1$, $p < 0.001$) and had smaller core areas ($t_{22} = 2.27$, $p = 0.03$, Fig. 2). Estimated median core area of males was 4.5 times larger than females (95% confidence interval = 1.9, 10.8) after accounting for age (SEX + AGE model), although males, on average, were only 1.6 times heavier than females. Estimated median core area was positively correlated with % FOREST_COVER ($p = 0.03$, $r^2 = 0.17$), although this model had lower model weight compared to the models SEX + AGE or AGE (Table 4).

Movement and rest site reuse

Mean maximum daily distance traveled was higher for males (672 m; 95% confidence interval = 552 m, 792 m) compared to females (mean = 344 m; 95% confidence interval = 273 m, 415 m; Fig. 5); three males traveled > 1000 m in < 24 h, no female traveled > 500 m in 24 h. We had sufficient rest site reuse data (29.2 ± 6.3 resting locations per individual) to describe resting locations for ten individuals in the wet season but lacked sufficient data during the dry season and for adult females. Rest site reuse index was similar for all groups compared but mean reuse of resting sites by juvenile males (0.34 ± 0.06, n = 3) was slightly lower than that for juvenile females (0.45 ± 0.05, n = 2) and adult males (0.48 ± 0.07, n = 5). No individual used the same rest site as another individual. Short-tailed weasels most frequently used rest sites for a single day in the wet season (n = 186), but occasionally stayed in the same rest site for multiple consecutive days (two days, n = 42; three days, n = 6; four days, n = 1). We did not have sufficient data on individuals in the dry season to estimate reuse rates.

Discussion

Sex and cover type appeared to influence space use by short-tailed weasels. Cover type appeared to dictate female home range placement: females had small home ranges composed primarily of cover types not dominated by conifer forest (grass conifer, fields). In contrast, males selected grass
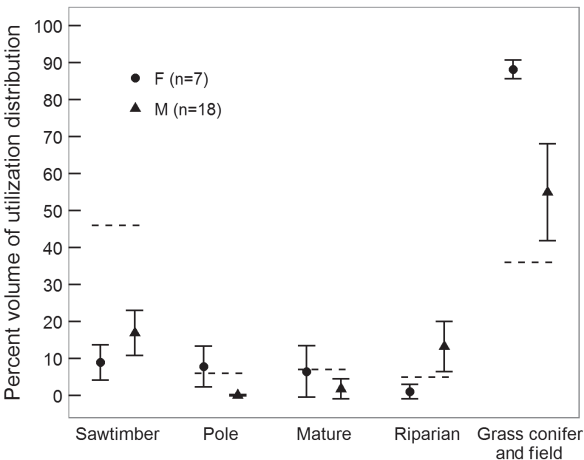

Figure 3. Mean and 95% confidence intervals of utilization distribution volume for female (F) and male (M) short-tailed weasels in six cover types (grass conifer and field were combined) in Corvallis, Oregon, USA, 2012–2013. Dashed line represents the percent composition of the study area for each cover type.
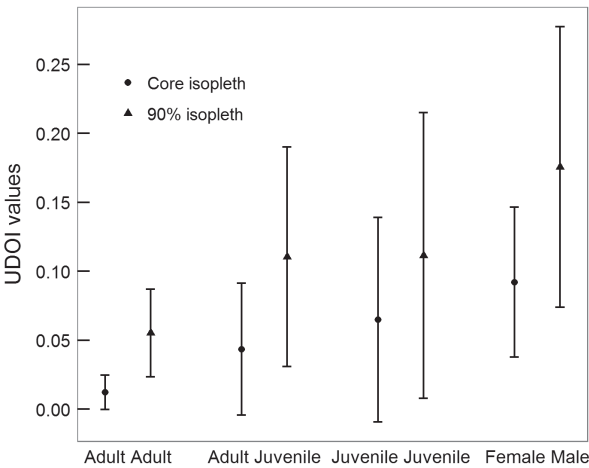

Figure 4. Space use overlap of short-tailed weasels based on the utilization distribution overlap index (UDOI) in Corvallis, Oregon, USA, 2012–2013. Dyads were Adult:Adult (n = 7, same sex), Adult:Juvenile (n = 12, same sex), Juvenile:Juvenile (n = 4, same sex), and Female:Male (n = 3, opposite sex) combinations of weasels that had home 90% isopleth home ranges that overlapped. Core range and 90% isopleth home ranges shown.

Table 4. A priori models used in analysis of CORE AREA of short-tailed weasels on the McDonald-Dunn Research Forest, Benton County, OR, USA. Models are arranged in order of increasing AICc values. Models with Delta AICc values <2 were considered competitive.

Models[1]	No. of parameters	AICc	Delta AICc	AICc Weight
SEX+AGE	4	70.71	0.00	0.75
SEX	3	73.09	2.38	0.23
%FOREST_COVER	3	78.43	7.72	0.02
AGE	3	82.42	11.71	0.00

[1]AGE is the categorical age of an individual, either adult or juvenile. %FOREST_COVER is the proportion of closed canopy vegetation within the home range (canopy cover was estimated for all vegetation >1 m tall).

conifer and fields but showed greater apparent flexibility, with greater use of other cover types. Our results are consistent with other studies which have observed stronger cover type selection by females (Lisgo 1999, Hellstedt and Henttonen 2006), which we suspect is largely driven by the high energy demands of providing for kits (Erlinge 1979) and the abundance of prey in early stage of plantation forest (Gomez and Anthony 1998). Both sexes, nonetheless, strongly selected the ephemeral early stage of managed forest (grass conifer; Table 2). Moreover, core areas increased with increasing proportion of conifer forest cover, although we could not discount that estimating core areas on an individual basis may have introduced additional variation into these estimates. Although short-tailed weasels are flexible in their space use, accommodating large home range sizes (Table 1), we suspect that home range sizes we observed are unlikely to be stable as early stage transitions to closed-canopy conifers (sawtimber), a cover type largely avoided by short-tailed weasels.

Spatial overlap of territories during our study was consistent with previously described patterns of intrasexual territoriality predicted to occur where prey resources are stable (Powell 1979, Debrot and Mermod 1983). Adults showed low intrasexual spatial overlap, particularly of high-use core areas within their home ranges. In contrast, intersexual spatial overlap was higher but highly variable (Fig. 4). Most studies have reported little intersexual spatial overlap (Sweden, 10% during the breeding season, Hellstedt and Henttonen 2006) or did not quantify it (Murphy and Dowding 1994, Smith et al. 2007), but observed low intrasexual overlap. We suspect intersexual overlap is often underestimated due to low capture rate of females (King 1975, King and Powell 2007), including in our study. Despite sampling limitations, adults in our study showed fairly consistent exclusive intrasexual territory use. The timing and duration of intrasexual territoriality remains relatively unexplored for weasels, particularly since stable prey availability, which is hypothesized to support stable social organization, is often either uncommon, or unknown by researchers.

Although we were unable to measure rest site reuse in the dry season, we propose that the frequent reuse of rest sites by short-tailed weasels in winter represents behavioral adaptations to cold temperatures. We observed that many of these sites were broadly associated with downed woody debris, logs, and occasionally hollows in live trees which may have provided insulating cover, although identifying the precise rest site structure was difficult in this system (Linnell 2014). Furthermore, reuse of resting locations may be a consequence of surplus killing of prey (Jedrzejewska and Jedrzejewski 1989), whereby weasels may be returning to or not leaving sites where they have cached food. Moreover, weasels may invest energy in certain resting locations when they insulate them with the fur and skin of their prey (Fitzgerald 1977). Reuse of modified rest sites may thus offer energetic benefits and be a familiar refuge where food can be stored to use during inclement weather. That familiar rest sites are important is supported by observations of weasels carrying prey up to 50 m to a rest site.

Tolerance of juveniles by territorial adults may differ by sex, leading to different dispersal strategies of juvenile males and females. Although weasels are capable of dispersing long distances (King and Powell 2007), most apparently do not (Erlinge 1977, Debrot and Mermod 1983), and either die or establish territories near natal areas. In our study, juvenile females appeared largely philopatric, and moved distances were similar to adult females (i.e. relatively short), whereas juvenile males moved greater mean distances, potentially seeking available territories over a larger area, while avoiding resident adult males. Despite differences in movement distances, juveniles of both sexes that remain near natal areas may have a fairly high probability of acquiring vacated adult territories and exploring breeding opportunities near natal areas due low annual survival of adults in this and other systems (Linnell et al. 2017).

Strong selection for early stage forest, particularly by females, and relatively small home ranges in that cover type suggest that the short-tailed weasels in our study probably reach their highest densities in early stage forest, similar to observations by Simms (1979b). The relatively short window (5–10 years) of availability of this cover type, however, indicates that short-tailed weasel populations almost certainly must shift space use in managed forests to track availability
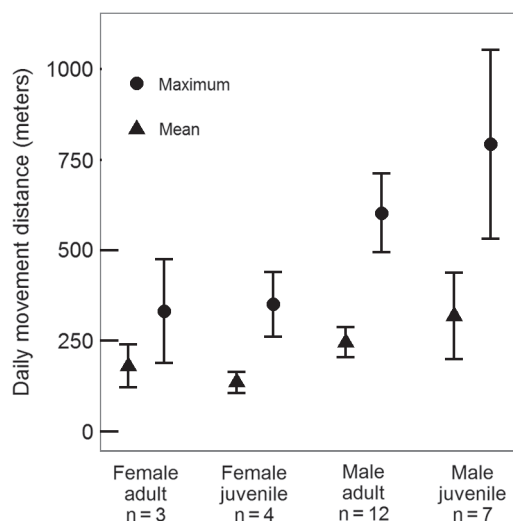

Figure 5. Mean maximum and mean daily movements (meters) by short-tailed weasels in Corvallis, Oregon, USA, 2012–2013 by sex (female (F); male (M)) and age class.

of potentially prey-rich early stage forest. Additional research on space use by weasels in these landscapes is needed, particularly on limitations to their dispersal and their establishment in landscapes dominated by intensively managed forests, such as the Coast Range of western Oregon.

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Supplementary material (available online as Appendix wlb-00270 at <www.wildlifebiology.org/appendix/wlb.00270>). Appendix 1.