

LANDSCAPE PROPORTIONS VERSUS MONTE CARLO SIMULATED HOME RANGES FOR ESTIMATING HABITAT AVAILABILITY

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Abstract: Wildlife researchers often test whether animals use resources disproportionately relative to availability (i.e., selectively). However, the traditional estimate of availability at the landscape scale (resource proportions on the landscape) may be inaccurate and lead to false conclusions. We calculated the chance of falsely finding selection (type I error rate) when the traditional estimate of availability is used. True availability was estimated by Monte Carlo simulations with randomly located home ranges and compared to the traditional estimate to calculate type I error rates. Tests were conducted with $\alpha = 0.05$ for different home range sizes (1 to 1,000 km²) and 4 habitat patterns. Landscape proportions did not equal proportions of habitats in random home ranges (traditional estimate \neq true availability). Type I error rates were ≥ 0.24 and increased with number of animals tested and decreased with home-range size and number of habitats. Therefore, researchers should use randomly located home ranges instead of landscape proportions to estimate availability at the landscape scale. We evaluated a goodness-of-fit test for comparing habitat proportions between randomly located home ranges and observed home ranges. Type I error rates for this method were ≤ 0.08 , regardless of number of animals, home range size, and number of habitats tested. We evaluated this method for 2 species with different home range sizes and predicted habitat selection patterns: mountain lions (*Puma concolor*, ≈ 700 km², relatively nonselective) and mule deer (*Odocoileus hemionus*, ≈ 16 km², relatively selective). This method yielded results consistent with predictions, whereas the traditional method using landscape proportions to estimate availability did not. Randomly located, simulated home ranges are superior to landscape proportions for estimating availability.

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Selection analysis, which compares use of habitats relative to their availability, is a common method for assessing importance of habitat to animals (Millspaugh and Marzluff 2001, Manly et al. 2002). For example, 21 habitat selection studies were published in *The Journal of Wildlife Management* between January 2001 and October 2003. Animals may select habitats at several spatial scales: geographical (1st order), landscape (2nd order), home range (3rd order), and microsite (4th order) (Johnson 1980). Most authors recommend examining selection at more than 1 scale (Erickson et al. 2001, Garton et al. 2001, Cooper and Millspaugh 2001, Manly et al. 2002). Researchers typically examine home range and landscape selection concurrently (e.g., see Wielgus et al. 2002, Wielgus and Vernier 2003).

When animals are not selective, we expect them to use habitats in proportion to their availability (Aebischer et al. 1993, Allredge et al. 1998). At

the home-range scale, use is measured by the proportion of animal observations in each habitat. Under the no-selection (null) model, these observations should be located independent of the distribution of habitats, so availability is measured by the proportion of each habitat in the home range. Both measures are made within the same area (the home range) and therefore comparable (Manly et al. 2002).

At the landscape scale, nonselective animals should locate their home ranges independent of the distribution of habitats on the landscape. Use is measured by the proportion of each habitat in the home range and availability by the proportion of each habitat on the landscape, approximated by a subjectively defined study site (Allredge and Ratti 1992, Cooper and Millspaugh 2001, Erickson et al. 2001, Manly et al. 2002). These measures are made within areas of different size, however, and therefore not comparable. Animals do not normally roam across the entire landscape but instead limit their movements to a home range-sized area, so habitat proportions in the study site are an unrealistic measure of availability.

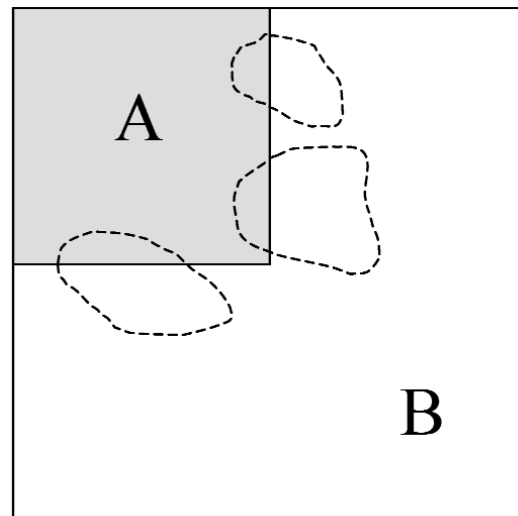
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This traditional measure of landscape availability also ignores confounding effects of spatial pattern on habitat proportions (Porter and Church 1987, Otis 1998, Wilson et al. 1998). A home range-sized area cannot have a habitat composition similar to the larger study site when habitats are aggregated or clumped on the landscape (Johnson 1980, Porter and Church 1987, Wilson et al. 1998, Millspaugh and Marzluff 2001). Consider a habitat (A) that comprises 25% of the landscape but is aggregated in one patch (Fig. 1A). The traditional estimate of availability (0.25, the proportion of habitat A on the landscape) could be realized only if a home range was located on the edge between habitats A and B, which would not be random relative to habitat. In a landscape with 4 equally abundant, aggregated habitats (Fig. 1B), proportions of habitats in a home range and on the landscape could be equal only if the home range was located where the 4 habitats abutted. Such a nonrandom location would be contrary to the null model we are trying to test. Habitat proportions in home ranges can equal proportions on the landscape only when habitats are uniformly distributed in patches that are small relative to the home range size (Wilson et al. 1998). Therefore, the traditional estimate of availability may not reliably predict home-range compositions of nonselective animals and may lead to false or spurious conclusions about selection. Availability estimates need to be spatially explicit (Shulz and Joyce 1992).

Wilson et al. (1998) proposed using Monte Carlo simulations with randomly placed home ranges to generate spatially explicit estimates of availability. They randomly located simulated home ranges across the landscape, then constructed a confidence interval for each habitat from the frequency distribution of proportions of the habitat within the random home ranges. These spatially explicit measures of availability were then compared to habitat proportions in animal home ranges to test whether use was selective (different from random) for each animal (Wilson et al. 1998). Multiple habitats could be tested simultaneously by adjusting confidence limits for number of habitats, following Sokal and Rohlf (1981). However, each animal was tested individually. If numerous animals were studied, treating them as independent samples in a single test would be preferable.

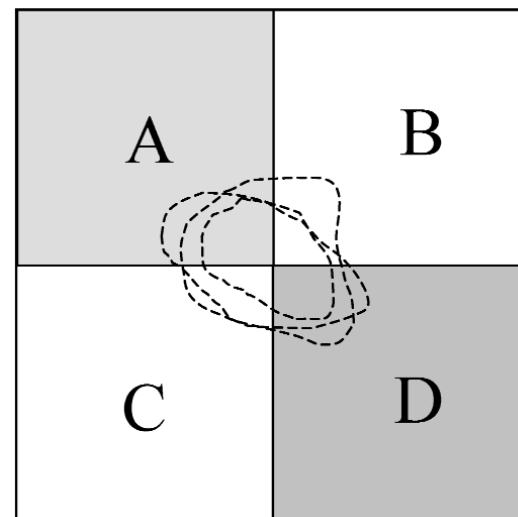
Despite the concerns raised by Porter and Church (1987), Shulz and Joyce (1992), Wilson et al. (1998), and Millspaugh and Marzluff (2001),



(A) Landscape proportions and estimated availability:

$$A = 0.25$$

$$B = 0.75$$



(B) Landscape proportions and estimated availability:

$$A = 0.25$$

$$B = 0.25$$

$$C = 0.25$$

$$D = 0.25$$

Fig. 1. Some possible locations of home ranges (dashed polygons) containing proportions of habitats equal to the proportion of the landscape occupied by each habitat (traditional estimate of availability at the landscape scale) for (A) a hypothetical landscape containing of 25% of 1 aggregated habitat, and (B) a hypothetical landscape with 4 equally abundant, aggregated habitats.

Table 1. Habitat composition of study site in northeastern Washington and northern Idaho, USA, and southeastern British Columbia, Canada, 1998–2001.

Habitat	% Area
Alpine: tree canopy $\geq 10\%$, whitebark pine (<i>Pinus albicaulis</i>) $\geq 50\%$ of canopy	7.2
Recently Burned/Logged	9.3
Cedar–Hemlock: tree canopy $\geq 10\%$, western redcedar (<i>Thuja plicata</i>) and western hemlock (<i>Tsuga heterophylla</i>) combined $\geq 50\%$ of canopy	7.5
Hardwood/Riparian: any deciduous component (balsam poplar [<i>Populus balsamifera</i>], aspen [<i>P. tremuloides</i>], mountain alder [<i>Alnus incana</i>], paper birch [<i>Betula papyrifera</i>], water birch [<i>B. occidentalis</i>], arbutus/madrone [<i>Arbutus menziesii</i>]) with $\geq 25\%$ vegetative cover	2.8
Lodgepole Pine/Larch: tree canopy $\geq 10\%$, lodgepole pine (<i>Pinus contorta</i>) and western larch (<i>Larix occidentalis</i>) combined $\geq 50\%$ of canopy	14.3
Mixed Species Dry Forest: tree canopy $\geq 10\%$, dry-site species (Douglas fir [<i>Pseudotsuga menziesii</i>] or ponderosa pine [<i>Pinus ponderosa</i>] but may include grand fir [<i>Abies grandis</i>], lodgepole pine, white pine [<i>P. monticola</i>], or larch in lesser amounts) combined $\geq 50\%$ of canopy	17.3
Mixed Species Moist Forest: tree canopy $\geq 10\%$, typical wet-site species (hemlock or cedar but may include grand fir, lodgepole pine, white pine, or larch in lesser amounts) combined $\geq 50\%$ of canopy	5.4
Nonforested: $< 25\%$ vegetative cover	9.6
Unclassified: no habitat data	2.7
Regenerating Forest: tree canopy $\geq 10\%$ of any sapling- or pole-sized (< 12 cm diameter at breast height) tree	2.1
Spruce–Fir: tree canopy $\geq 10\%$, subalpine fir (<i>Abies lasiocarpa</i>) and Engelmann spruce (<i>Picea engelmannii</i>) combined $\geq 50\%$ of canopy	14.0
Shrub: woody vegetation with $< 10\%$ tree canopy	3.9
Water	3.8

little attention has been paid to the potential problems of comparing home ranges to landscapes (Manly et al. 2002) and type I error rates have not been quantified for tests using traditional versus spatially explicit estimates of availability. Our first objective was to calculate type I error rates (probability of falsely finding selection) for the traditional estimate of availability for home-range sizes between 1 and 1,000 km² and different habitat patterns. Our second objective was to determine whether a goodness-of-fit test using animals as independent sample units would work for the Monte Carlo simulation procedure proposed by Wilson et al. (1998). We estimated type I error rates for the Monte Carlo procedure for the same habitat patterns, home-range sizes, and sample sizes used to evaluate type I error rates for the traditional availability esti-

mate. We then evaluated the effectiveness of the Monte Carlo method using empirical data for a species with a relatively large (> 500 km²) home range (mountain lion) and a species with a relatively small (< 20 km²) home range (mule deer).

METHODS

We used an existing habitat map to obtain results directly applicable to a real-world situation (Turner 1989, McClean et al. 1998). Simulating habitat patterns would allow comparisons over a broader range of hypothetical conditions, but was beyond the scope of this study. Our study site was located in northeastern Washington and northern Idaho, USA, and southeastern British Columbia (B.C.), Canada, between 48.0–49.8° north latitude and 116.0–117.5° west longitude. The U.S. Forest Service (USFS) and B.C. Ministry of Sustainable Resource Management mapped habitats by interpreting aerial photographs, classifying LANDSAT images, and measuring vegetation in sample plots. Species, canopy closure and vegetation height were used to identify 13 habitats (Table 1).

We conducted Monte Carlo simulations in the Geographic Information System (GIS) ARC/INFO and ArcView (Environmental Systems Research Institute, Redlands, California, USA) by randomly placing 1,000 home ranges on the landscape and calculating habitat proportions in each. Home ranges were constructed by choosing random points on the landscape and generating circular areas around them equal to the desired size of the simulated home range. Simulated home ranges were allowed to overlap. Twenty-eight sets of random home ranges were generated to simulate small (1, 2, 3, ..., 9 km²), medium (10, 20, 30, ..., 90 km²), and large (100, 200, 300, ..., 1,000 km²) home ranges. Our sample size ($n = 1,000$ simulated home ranges) for each set was based on preliminary tests using 10 to 10,000 random home ranges from which we concluded that 1,000 random home ranges adequately sampled habitat variability while minimizing simulation time. Because of the large number of spatial overlays required, we wrote an Arc Macro Language (AML) program in ARC/INFO to automate the process.

We compared habitat proportions in the randomly located home ranges to proportions on the landscape to evaluate the traditional estimate of availability for predicting use by nonselective animals. Subsets of simulated home ranges were selected at random as hypothetical groups of sample animals, similar to Pendleton et al.

(1998). We then used Friedman's (1937) non-parametric Analysis of Variance (ANOVA) to test whether selection differed among habitats for each subset of "animals" (Alldredge and Ratti 1986). No selection should have been detected because use was determined for randomly placed home ranges. We calculated the proportion of ANOVA tests for which the null hypothesis was rejected ($P \leq 0.05$) to find the probability of committing a type I error (falsely concluding that habitat selection had occurred). The procedure was repeated for each home-range size. Number of animals sampled and habitats assessed affects the ability to detect selection (i.e., statistical power or type II error rate; Alldredge and Ratti 1986) but should not affect type I error rates unless availability estimates are biased. To test these assumptions, we repeated the type I error analysis for 3 subset sizes (10, 20, and 40 "animals") and for 2 sets of habitats (7 vs. 13).

Abundance and distribution of a habitat could affect proportions in randomly located home ranges and, therefore, reliability of the traditional estimate of habitat availability (proportion of the landscape). The set of 13 habitats included spruce–fir, which was relatively abundant (14% of the study site; Table 1) and moderately aggregated (Fig. 2A); cedar–hemlock, which was moderately abundant (8% of the study site) but more aggregated (Fig. 2B); and shrub, which was rare (4% of the site) but more uniformly distributed (Fig. 2C). Spatial characteristics may differ dramatically between

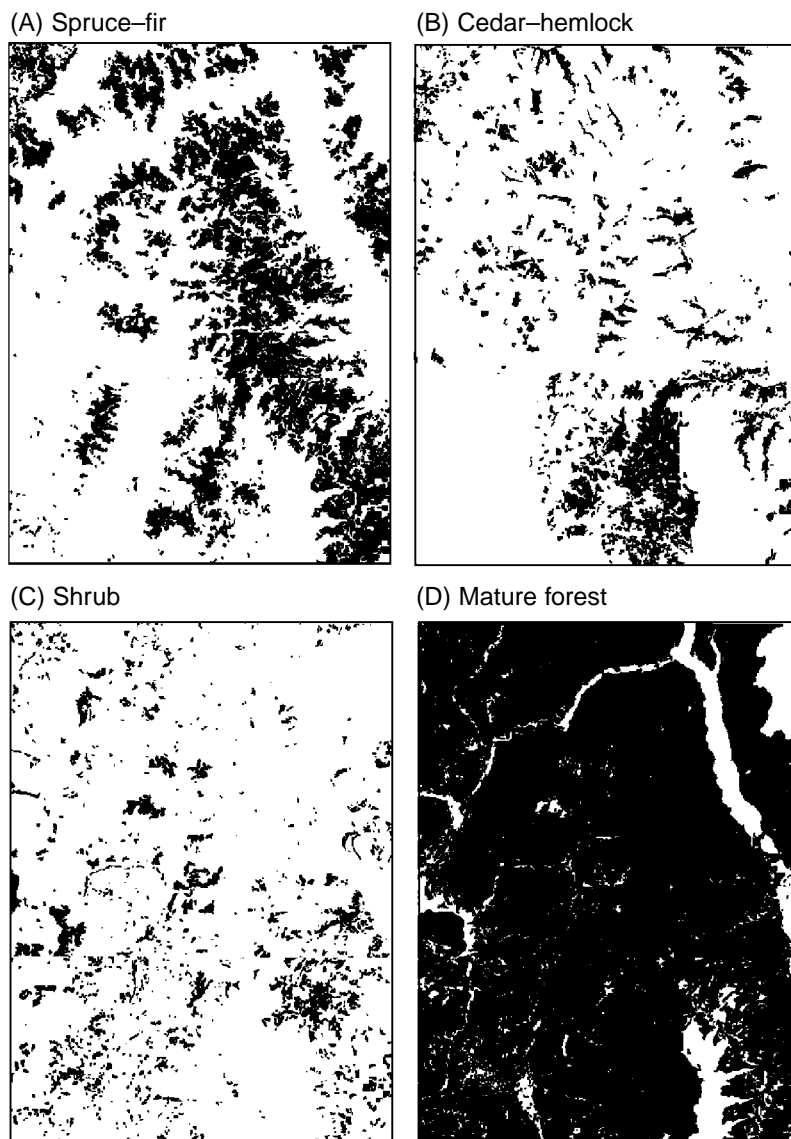


Fig. 2. Spatial distribution of 4 habitats used to assess availability estimates: (A) spruce–fir, comprising 14% of the study site and moderately aggregated; (B) cedar–hemlock, comprising 8% of the study site and more aggregated than spruce–fir; (C) shrub, comprising only 4% of the study site but more uniformly distributed than spruce–fir or cedar–hemlock; and (D) mature forest, comprising 62% of the study site and contiguous across the landscape.

abundant and rare habitats. It is known from percolation theory that randomly distributed habitats that occupy $>59\%$ of a landscape tend to form large, contiguous patches spanning the landscape (Gardner et al. 1987). Therefore, we wanted to include an abundant habitat in our analyses. None of the 13 habitats occupied $>59\%$ of the landscape (Table 1), so we grouped several (including spruce–fir and cedar–hemlock) into a new habitat called mature forest, defined as $\geq 10\%$ canopy cover by trees >12 cm diameter at

breast height. Mature forest occupied 62% of the study site and was contiguous across the landscape (Fig. 2D). The second set of habitats ($n = 7$) used to evaluate the traditional estimate of availability consisted of mature forest, recently burned/logged forest, nonforested, regenerating forest, shrub, water, and unclassified (no data).

Our second objective was to devise a method for testing landscape-scale selection using animals as replicates (i.e., 1 test per habitat across ≥ 2 animals) when Monte Carlo simulations with randomly placed home ranges are used to generate spatially explicit estimates of availability. We estimated the cumulative distribution function (CDF) for a given habitat using randomly placed home ranges equal in size to the average home range of the species being tested. This random CDF predicted habitat proportions in home ranges with no selection (random use = availability). We then estimated a second CDF from the real (observed) animal home ranges and used a Kolmogorov goodness-of-fit test (Conover 1980:344–348) to determine whether it was different from the random CDF. Failure to reject the null hypothesis would support the no-selection model. If the null hypothesis was rejected, we compared the probability-weighted, mean value between observed and random CDFs and examined the CDF plots to determine how observed and random use were different.

Type I error rates for this proposed procedure were estimated using the same methods described above for the traditional estimate of availability. Simulated home ranges were located randomly within the study site and subsets of $n = 10, 20,$ and 40 “animals” used to test for selection. We conducted simulations using 4 home-range sizes (1, 10, 100, 1,000 km²) in 4 habitats (spruce–fir, cedar–hemlock, shrub, mature forest).

We used 2 species, mountain lions and mule deer, with different sized home ranges to evaluate the effectiveness of our proposed method. Seventeen mountain lions and 25 mule deer were radiotracked from 1998–2001 by Washington Department of Fish & Wildlife and Columbia Basin Fish & Wildlife Compensation Program. A 95% adaptive kernel (Worton 1989) was used to estimate a home range for each animal. Mean size of home ranges was 711 km² (SE = 207) for lions and 16 km² (SE = 3) for mule deer.

Location of mountain lion home ranges may be influenced by territoriality and land tenure (Seidensticker et al. 1973, Hemker et al. 1984, Laing and Lindzey 1993, Logan et al. 1996). Further, lions

are a generalist predator of white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and mule deer (Hornocker 1970, Spalding and Lesowski 1971, Toweill and Meslow 1977). Therefore, we did not expect to find strong patterns of habitat selection at the landscape scale for mountain lions. In contrast, mule deer are a herding species that selects for specific habitats that provide thermal and security cover and forage (Collins and Urness 1983, Carson and Peek 1987). We expected mule deer to be strongly selective for coniferous forest and riparian habitats at the landscape scale.

We compared results obtained from our CDF-comparison method with results obtained in tests using the traditional estimate of availability. For the latter tests, we used Johnson’s (1980) procedure, which compares the rank order of use to the rank order of availability because of its simplicity and frequent use in the wildlife literature (Alldredge and Ratti 1986). We did not question the validity of Johnson’s (1980) test, only the results obtained when the availability estimates used in the test are not spatially explicit and therefore, we hypothesized, inaccurate. We analyzed both sets of habitats ($n = 13$ and 7 habitats) used to calculate type I errors. Our CDF-comparison method examines habitats individually, requiring a researcher to select a subset of habitats a priori or to examine every habitat and adjust the experiment-wise error rate accordingly (e.g., Miller 1966). In contrast, Johnson’s (1980) method tests selection for all habitats simultaneously. Therefore, we analyzed all habitats with the proposed CDF-comparison method to obtain comparable results, but adjusted the rejection level (13 habitats, $\alpha = 0.05 / 13 = 0.004$; 7 habitats, $\alpha = 0.05 / 7 = 0.007$). This approach was conservative; most researchers would not test all habitats but instead identify a subset of important habitats to test based on previous studies or their specific hypotheses.

RESULTS

Although the traditional estimate of availability (proportions on the landscape) was 14.0% spruce–fir, 7.5% cedar–hemlock, and 3.9% shrub (Table 1), $\leq 20\%$ of random home ranges contained those habitat proportions and there was large variability in proportions of each habitat among random home ranges (Fig. 3). The distribution for mature forest was bimodal; $\geq 49\%$ of random home ranges contained either $\leq 40\%$ or

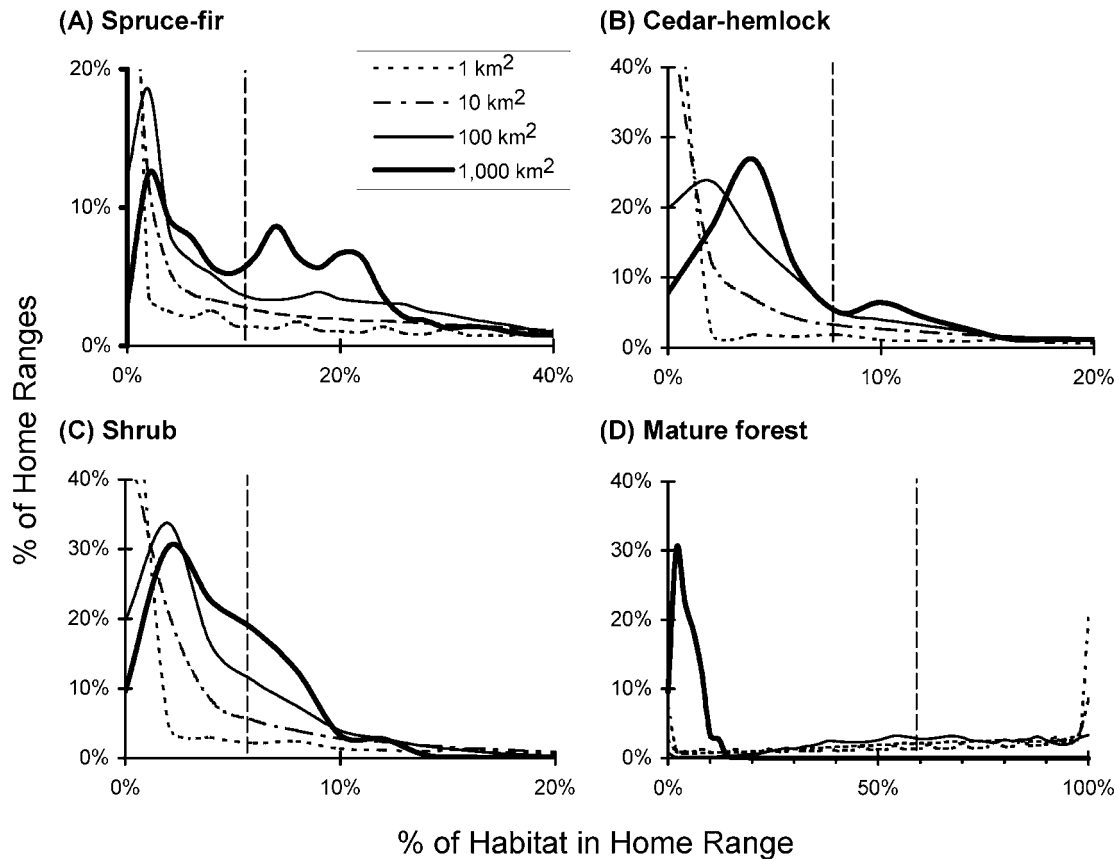


Fig. 3. Frequency distribution of 4 sizes (1, 10, 100, 1,000 km²) of randomly placed, simulated home ranges based on the proportion of spruce–fir, cedar–hemlock, shrub, and mature forest within them. Vertical, dashed lines indicate the proportion of the landscape occupied by each habitat (traditional estimate of availability at the landscape scale).

≥80% mature forest despite that its “availability” (proportion of the landscape) was 62%.

The weak relationship between habitat proportions on the landscape and true landscape-scale availability, measured from randomly located home ranges, resulted in high type I error rates for tests of habitat selection. The probability of falsely concluding that habitat selection had occurred ranged from 0.24 to 1.00 when the traditional method was used to estimate availability (Fig. 4). Type I error rates increased with number of animals sampled (block size) and decreased with number of habitats (treatments) tested and home-range size.

Type I error rates for the Monte Carlo CDF-comparison method were ≤0.08 and averaged 0.026 ($n = 48$, $SE = 0.003$) across all habitats, home-range sizes, and sample sizes (Fig. 5). As with the traditional method, mean error rate increased with sample size, but only from 0.023 ($n = 10$ animals) to 0.029 ($n = 40$). Home-range size had

more effect on type I error rate, which was greater for medium-sized home ranges (10–100 km²; $\bar{x} = 0.033$, $n = 24$, $SE = 0.004$) than for the smallest (1 km²; $\bar{x} = 0.018$, $n = 12$, $SE = 0.005$) or largest (1,000 km²; $\bar{x} = 0.019$, $n = 12$, $SE = 0.003$) home ranges. Mean error rate was greatest in mixed forest (0.034) and spruce–fir (0.030) and least in cedar–hemlock (0.022) and shrub (0.018; Fig. 5).

Our CDF-comparison method detected the expected patterns of habitat selection by mountain lions and mule deer. From the set of 13 habitats, lions used only mixed-species moist forest selectively ($T = 0.444$, $n = 17$, $P = 0.002$). The mean observed use of this habitat was 11.7, compared to 5.3 for the random CDF (Table 2, Fig. 6). By contrast, mule deer used 7 of the 13 habitats selectively. Mule deer did not use cedar–hemlock ($T = 0.250$, $n = 25$, $P = 0.077$), lodgepole pine/larch ($T = 0.298$, $P = 0.019$), mixed-species dry forest ($T = 0.270$, $P = 0.044$), mixed-species moist forest ($T = 0.269$, $P = 0.045$), spruce–fir ($T = 0.269$, $P = 0.045$),

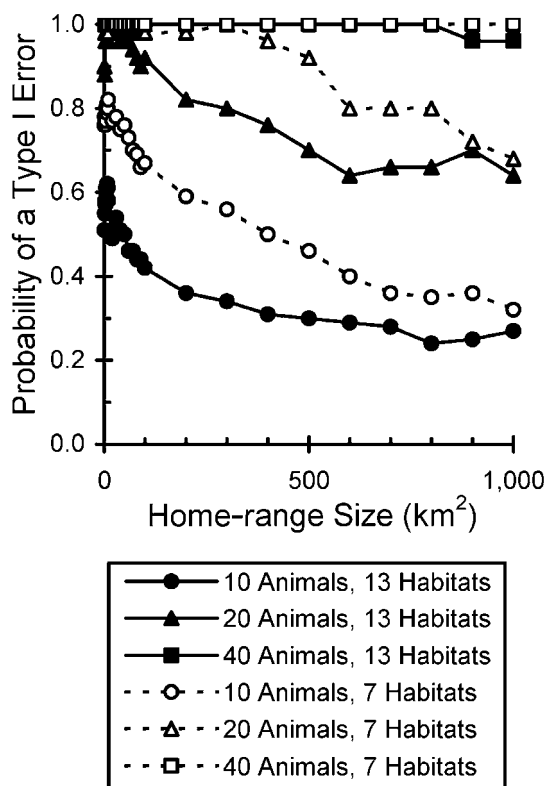


Fig. 4. Probability of committing a type I error (falsely concluding that animals use habitats selectively) when using the traditional estimate of landscape-scale availability (proportion of the landscape occupied by each habitat) for 3 sample sizes ($n = 10, 20, 40$ animals) and home-range sizes from 1 to 1,000 km² for 2 sets of habitats (7 vs. 13).

or shrub ($T = 0.302, P = 0.017$) selectively. However, note that without our conservative adjustment of the rejection level, use of all habitats except cedar–hemlock ($P = 0.077$) would have been interpreted as selective (Table 2). Mule deer selected for recently burned/logged, hardwood–riparian, unclassified habitat, and regenerating forest ($T \geq 0.503, P \leq 0.001$; Fig. 7A–D) and against water ($T = 0.396, P < 0.001$; Fig. 7E). Mule deer also used alpine and nonforested habitats selectively ($T \geq 0.386, P \leq 0.001$; Table 2), but the selection pattern was more complicated than use \neq random. For alpine habitat (Fig. 7F), observed means were similar for mule deer versus random CDFs (5.5 vs. 6.7, respectively), but the proportion of alpine habitat within the home range varied less among mule deer home ranges (0.0–14.8% of the home range was alpine) compared to random home ranges (0.0–86.9% of the home range was alpine). For nonforested habitats (Fig. 7G), observed means were similar for

mule deer versus random CDFs (8.2 vs. 10.2, respectively), but the proportion of nonforested habitat in the home range varied less among mule deer (4.2–24.9% of the home range was nonforested) compared to random home ranges (0.0–85.2%). Therefore, although mean proportions in observed versus random home ranges were similar for these 2 habitats, there was less variability in alpine and nonforested habitat proportions among mule deer home ranges than among random home ranges.

Lions did not use any of the 7 habitats selectively ($P \geq 0.091$, Table 2). Mule deer did not use mature forest selectively ($T = 0.305, n = 25, P = 0.015$; rejection level = 0.007). Results for the other 6 habitats, which already were tested from the set of 13 habitats, did not change by adjusting the rejection level to account for fewer habitats tested.

We obtained different selection results using the traditional method to estimate landscape-scale availability. The traditional method indicated strong selection by both species ($P \leq 0.008$), whereas our CDF comparisons indicated that lions responded to only 1 of 13 (or 0 of 7) habitats (Table 2). The traditional method also indicated that mule deer avoided spruce–fir habitat, whereas the CDF test detected no selection. The Johnson (1980) rank preference test orders habitats by use (the proportion in the home range) relative to availability (the proportion in the study site) then allows pairwise comparisons of specific habitats. Spruce–fir was ranked 10 out of 13, implying that mule deer selected against it (use < availability).

DISCUSSION

Our first objective was to determine whether the traditional estimate of landscape-scale availability (proportions of the landscape occupied by each habitat) reliably predicts habitat proportions in randomly located home ranges and, therefore, nonselective use by animals. We found large variability in habitat proportions within random home ranges, often consistently different from habitat proportions on the landscape. Variability in habitat proportions among random home ranges was negatively related to home-range size and positively related to habitat abundance. Many random home ranges contained either 0% or 100% of a habitat. Habitats that are clumped tend to have greater inter-patch distances (Gustafson and Parker 1992) and therefore larger gaps in which home ranges could occur and contain 0% of the habitat. Alternatively, for small home ranges,

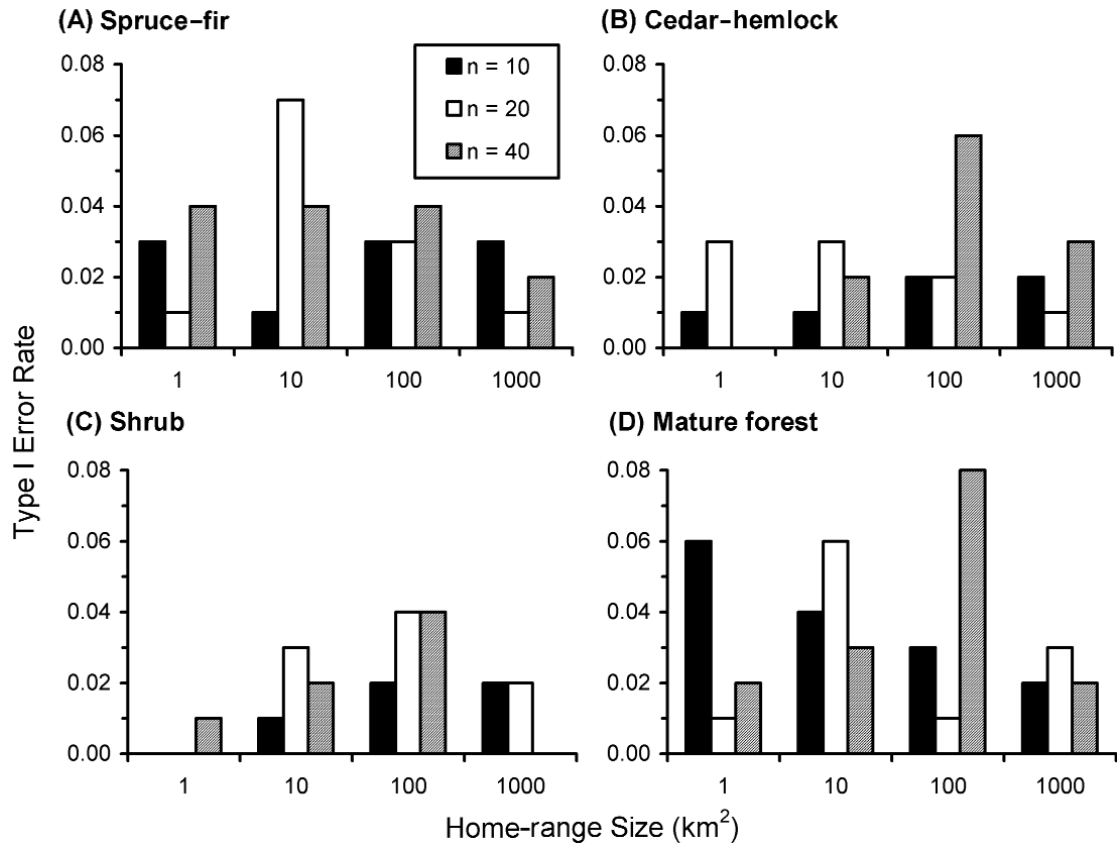


Fig. 5. Probability of committing a type I error (falsely concluding that animals used habitat selectively) when using randomly located, simulated home ranges to estimate landscape-scale availability for 3 sample sizes ($n = 10, 20, 40$ animals) and 4 home-range sizes (1, 10, 100, 1,000 km²) for A) spruce-fir, B) cedar-hemlock, C) shrub, and D) mature forest habitat.

some occurred entirely within 1 habitat patch, as postulated by Gardner et al. (1987). We concluded that the traditional method for estimating landscape-scale availability was unreliable for all home-range sizes and habitats examined but especially for small home ranges and abundant, aggregated habitats. Our results demonstrate the validity of the conclusions of Wilson et al. (1998) that estimates of availability that do not account for the spatial distribution of habitats or the area-restricted nature of animal movements do not accurately predict habitat proportions in home ranges of nonselective animals.

Our estimated type I error rates supported Porter and Church's (1987) and Wilson et al.'s (1998) proposition that the traditional method for estimating habitat availability at the landscape scale provides biased tests of selection. A type I error occurs when the null hypothesis (H_0 : no selection) is falsely rejected. Randomly placed home ranges should not, by definition, exhibit habitat selection. Therefore, we should have

rejected the null hypothesis in 5% ($\alpha = 0.05$) of our tests comparing habitat proportions between the landscape and random home ranges. In contrast, we rejected the null hypothesis for $\geq 24\%$ of tests with large (≥ 800 km²) home ranges and $\geq 42\%$ for small (≤ 100 km²) home ranges when a rejection level of $P \leq 0.05$ was used. These high type I error rates indicate that comparing habitat proportions in home ranges (use) to proportions on the landscape (traditional estimate of availability) often results in a much greater probability of falsely concluding that selection had occurred than the usually specified $\alpha = 0.05$, because landscape proportions may be biased estimates of true availability. Further, we found that type I error rates increased with practices commonly used to improve ability of detecting selection; increasing number of animals and reducing number of habitats (treatments). When the estimate of availability is biased, increasing sample size (number of animals tested) magnifies the effect of the bias, increasing the chance of committing a

Table 2. Selection for 13 versus 7 habitats analyzed using Johnson's (1980) rank preference test (Rank^a) with the traditional measure of habitat availability (proportions of habitats on the landscape) and analyzed using a goodness-of-fit test^b with availability estimated from 1,000 randomly placed, simulated home ranges for 17 mountain lions and 25 mule deer in northeastern Washington and northern Idaho, USA, and southeastern British Columbia, Canada.

Habitat ^c	13 types								7 types							
	Lions				Mule deer				Lions				Mule deer			
	Rank ^d	T	P	S	Rank ^e	T	P	S	Rank ^f	T	P	S	Rank ^g	T	P	S
ALPINE	13 ^D	0.40	0.006	0	6 ^D	0.42	<0.001	+/-								
CH	7 ^{B,C}	0.37	0.013	0	9 ^D	0.25	0.077	0								
HR	1 ^A	0.20	0.488	0	1 ^A	0.65	<0.001	+								
LL	10 ^{C,D}	0.31	0.064	0	7 ^D	0.30	0.019	0								
MDF	11 ^{C,D}	0.20	0.460	0	13 ^E	0.27	0.044	0								
MMF	2 ^{A,B}	0.44	0.002	+	8 ^D	0.27	0.045	0								
SF	9 ^{C,D}	0.16	>0.500	0	10 ^D	0.27	0.045	0								
MF									4 ^{B,C}	0.21	0.405	0	4 ^B	0.31	0.015	0
BL	12 ^{C,D}	0.20	0.462	0	4 ^C	0.51	<0.001	+	7 ^D	0.20	0.462	0	3 ^A	0.51	<0.001	+
NF	8 ^{C,D}	0.25	0.202	0	11 ^D	0.39	<0.001	+/-	6 ^{C,D}	0.25	0.202	0	6 ^B	0.39	<0.001	+/-
UNC	3 ^{A,B}	0.29	0.098	0	3 ^B	0.71	<0.001	+	2 ^A	0.29	0.098	0	2 ^A	0.71	<0.001	+
RF	4 ^{A,B}	0.29	0.091	0	2 ^B	0.50	<0.001	+	1 ^A	0.29	0.091	0	1 ^A	0.50	<0.001	+
SHRUB	6 ^B	0.14	>0.500	0	5 ^C	0.30	0.017	0	5 ^{B,C,D}	0.14	>0.500	0	5 ^B	0.30	0.017	0
WATER	5 ^B	0.16	>0.500	0	12 ^D	0.40	<0.001	-	3 ^{A,B}	0.16	>0.500	0	7 ^C	0.40	<0.001	-

^a Habitats were ranked from least to most selected. Selection ranks were not different ($P > 0.05$) between habitats with the same letter in the same column.

^b A Kolmogorov goodness-of-fit test compared a cumulative distribution function (CDF) for the random home ranges to a CDF for each species and habitat. The Kolmogorov test statistic (T), P -value (P), and relative selection (based on observed means of CDFs) are given. Rejection levels were adjusted for number of comparisons (13 tests, $\alpha = 0.004$; 7 tests $\alpha = 0.007$). The selection symbol (S) indicates whether observed home ranges contained similar (0), larger (+), or smaller (-) proportions of the habitat compared to random home ranges. For "+/-" habitats, observed home ranges all contained moderate proportions of the habitat relative to random home ranges, most of which contained either 100% or 0% of the habitat.

^c CH = cedar-hemlock, HR = hardwood-riparian, LL = lodgepole pine-larch, MDF = mixed dry forest, MMF = mixed moist forest, SF = spruce-fir, MF = mixed forest, BL = burned-logged, NF = nonforested, UNC = unclassified, RF = regenerating forest (trees <12 cm dbh).

^d $F = 11.21$; $df = 12, 5$; $P = 0.008$.

^e $F = 57.22$; $df = 12, 13$; $P < 0.001$.

^f $F = 9.96$; $df = 6, 11$; $P < 0.001$.

^g $F = 46.87$; $df = 6, 19$; $P < 0.001$.

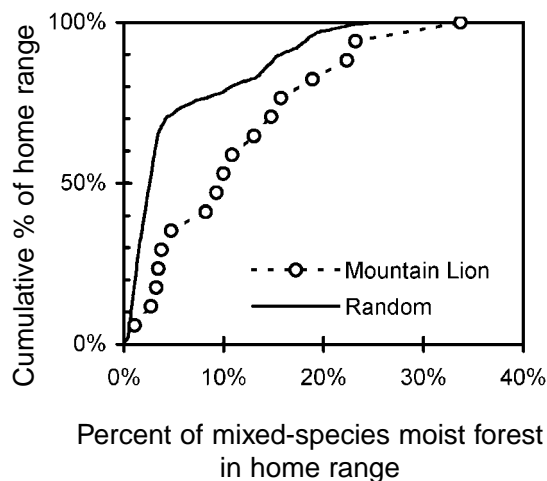


Fig. 6. Selection for mixed-species moist forest at the landscape scale by 17 mountain lions in northeastern Washington and northern Idaho, USA, and southeastern British Columbia, Canada. Selection was tested by comparing the cumulative distribution function (CDF) for mountain lions with a CDF generated from 1,000 Monte Carlo simulations of randomly placed home ranges.

type I error. When we used 40 animals to test selection, we found a type I error rate of ≥ 0.88 . Reducing number of treatments (habitats) resulted in greater perceived selection because smaller differences were needed to reject the null hypothesis.

Biased estimates of habitat availability may also increase the chance of committing a type II error (failing to detect selection). If habitat proportions in animal home ranges are similar to proportions on the landscape and landscape proportions are used to estimate availability, we would conclude no selection (use = availability). However, if landscape proportions are inaccurate and biased estimates of availability, then both landscape proportions and proportions of habitats in animal home ranges will not equal true availability and we should conclude that selection is occurring.

Our second objective was to devise an alternate method for estimating habitat availability at the landscape scale and to evaluate type I error rates for this method. Comparing observed and expected cumulative distribution functions (CDFs), the

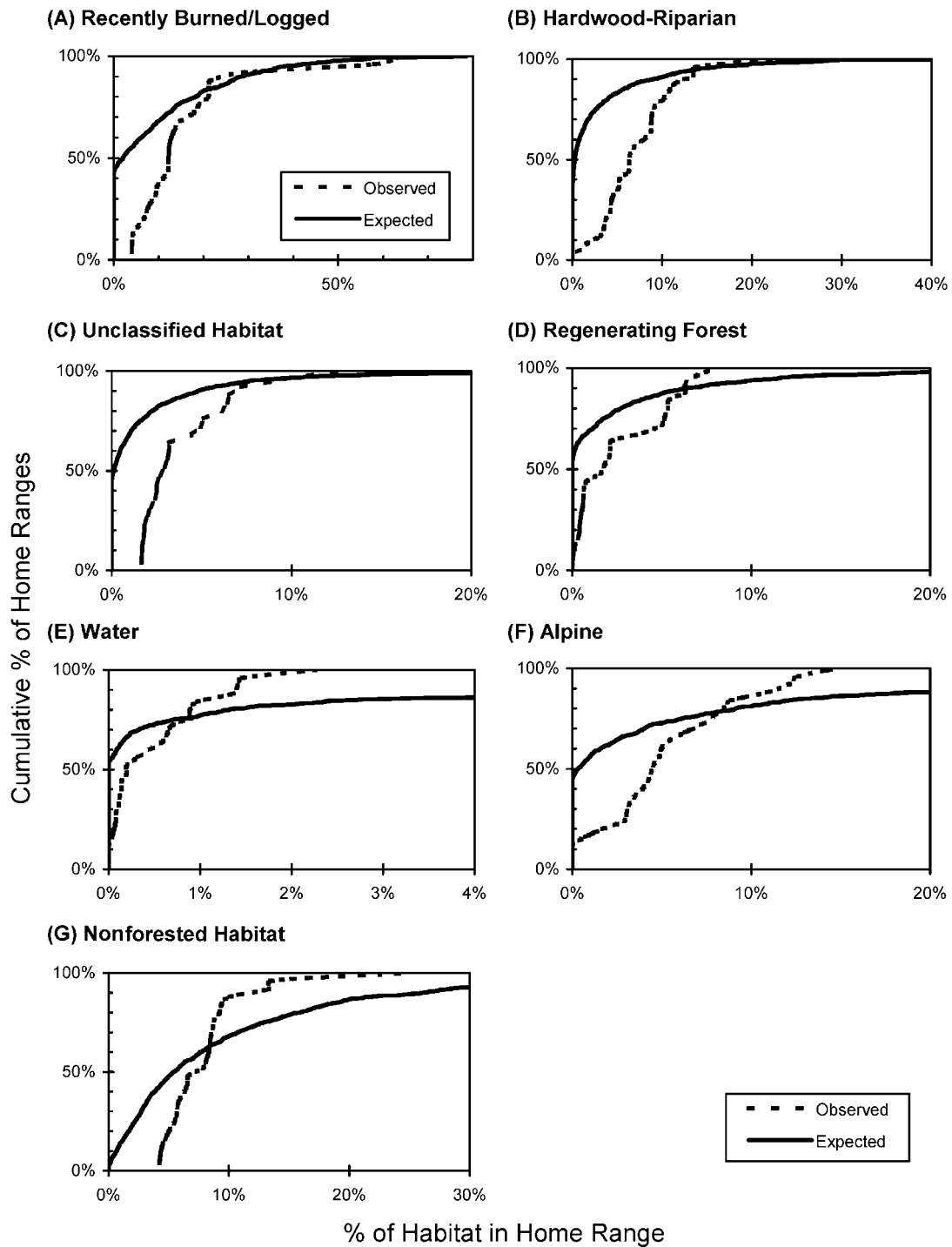


Fig. 7. Selection for 7 habitats: (A) recently burned/logged, (B) hardwood-riparian, (C) unclassified habitat, (D) regenerating forest, (E) water, (F) alpine, and (G) non-forested habitats at the landscape scale by 25 mule deer in northeastern Washington, northern Idaho, and southeastern British Columbia. Selection was tested for each habitat by comparing the cumulative distribution function (CDF) for mule deer (dotted line) with a CDF generated from 1,000 Monte Carlo simulations of randomly placed home ranges (solid line).

latter generated through Monte Carlo simulations with randomly placed home ranges, resulted in type I error rates ≤ 0.08 , and averaging 0.026, across all sample sizes, home-range sizes, and habitats tested. The Monte Carlo method was also much more effective than tests using the traditional method to estimate availability (landscape proportions). As predicted, our CDF comparisons indicated that mountain lions, a generalist predator (Hornocker 1970, Spalding and Lesowski 1971, Toweill and Meslow 1977), were not strongly selective at the landscape scale. In contrast, mule deer, a habitat specialist (Collins and Urness 1983, Carson and Peek 1987), used almost every habitat selectively.

A perceived problem with our CDF-comparison method might be that considering habitats individually ignores the multivariate nature of selection data (Thomas and Taylor 1990). Researchers often want to compare selection among habitats to assess relative importance, but adjusting the rejection level for a large number of CDF comparisons may make differences difficult to detect. However, even after conservatively adjusting our rejection level for 13 habitats to $P \leq 0.004$, we still detected selection by mule deer for 7 habitats. Further, testing a subset of a priori chosen habitats might make more sense at the landscape scale. Animals cannot alter the mix of habitats within their home range, only its boundaries and location (Garshelis 2000). Therefore, assessing selection for all habitats at the landscape scale may be misleading because habitat quality is confounded with distribution and spatial configuration. A multi-scale approach is critical in assessing wildlife-habitat relationships (Kotliar and Wiens 1990, Aebischer et al. 1993, McLean et al. 1998, Otis 1998). Researchers can test a subset of habitats at the landscape scale using our proposed CDF-comparison method, which accounts for the spatially explicit availability of habitats on the landscape, then simultaneously assess selection among all habitats within the home range (i.e., at a finer scale). When use is determined by point observations (e.g., telemetry locations) rather than by polygons (home ranges), availability estimates do not need to be spatially explicit because each point can be located independent of habitat.

Selection tests that use P -values to reject null hypotheses of random habitat use are considered by some authors (e.g., Johnson 1999, Anderson et al. 2000, Anderson and Burnham 2002, Manly et al. 2002) to be less useful or inappropriate for investigating wildlife-habitat relationships compared to model-evaluation methods based on

Information Criteria. Regardless of whether AIC or traditional statistical models are used, the problem with using landscape proportions to estimate availability is with the measure, not the statistical method. All statistical procedures that incorporate measures of landscape-scale availability, including resource selection functions (Manly et al. 2002) and models evaluated with AIC, could provide spurious results. We used a simple selection test to demonstrate the flaws with the traditional estimate of landscape availability because selection methods are familiar to biologists and easy to understand. Further, the type I error rate associated with selection tests was an effective tool for demonstrating the magnitude of the problem with the traditional estimate of landscape availability.

Landscape-scale analysis is a critical tool for effectively managing large areas for wildlife, habitat, and other natural resources (Turner 1989, Fahrig and Merriam 1994). Despite numerous problems with selection analysis (e.g.; Kotliar and Wiens 1990, Aebischer et al. 1993, Alldredge et al. 1998, McLean et al. 1998, this paper), it still is a useful tool for investigating wildlife-habitat relationships. Determining whether animals selectively locate their home ranges in habitats that increase their fitness is fundamental to wildlife management plans that estimate maximum abundance of animals based on distribution and abundance of those habitats. Further, quantifying the habitat choices animals make provides a context for evaluating how those choices affect fitness.

We believe spatially explicit estimation of habitat availability determined through Monte Carlo simulations with randomly placed home ranges is a valuable method for investigating wildlife-habitat relationships. Before the widespread availability of computers and GIS software, methods requiring large numbers of simulations were impractical. Now any computer capable of running GIS software can readily simulate random home ranges. We wrote AML and Avenue code for our analyses only because we conducted simulations for 28 different-sized home ranges. A simpler method for simulating a single sized, circular home range is the nearest neighbor, moving window function in ARC/INFO grid or ArcView Spatial Analyst. Alternatively, irregular-shaped home ranges could be used with a simple code for batch processing.

MANAGEMENT IMPLICATIONS

Management of wildlife and habitat is focusing increasingly on large spatial scales. We believe the tools discussed here leverage the growing

abundance of regional and statewide habitat maps and the expanding capabilities of GIS to provide resource managers and wildlife researchers with the ability to more accurately determine how wildlife interacts with the landscape. Spatially explicit measures should be used instead of landscape proportions to make availability estimates more realistic and analysis results more reliable. Our CDF-comparison method will provide a robust assessment of whether animals select for specific habitats at the landscape scale.

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