Territorial significance of home range estimators for coyotes

John A. Shivik and Eric M. Gese

Abstract   Many home range estimators are available, but few studies have examined the biological significance of mathematically described land-use patterns. We directly observed coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming to produce home range estimates using the harmonic mean, adaptive kernel, and minimum convex polygon methods. We compared estimated home ranges of 8 coyotes to their observed territories for 2 packs during 3 years of observation. Based on analysis of individual coyotes, the 94%, 93%, and 96% contours best fit territorial delineation for the adaptive kernel, harmonic mean, and minimum convex polygon estimators, respectively. All estimators were able to fit home range contours to an actual territory, but differences in home range fit were apparent. Using analyses based on packs, the 94%, 94%, and 96% contours best fit the territorial boundaries for the adaptive kernel, harmonic mean, and minimum convex polygon estimators, respectively. Our inferences to other species and radiotelemetry data are limited, and we encourage further biological testing of mathematically devised behavioral measures. Because the minimum convex polygon best fit territorial boundaries in 4 out of 5 territorial observations, and because of its intuitive simplicity, we suggest that the 96% minimum convex polygon may be most appropriate to describe coyote home ranges relative to territory in similar studies.

Key words   adaptive kernel, *Canis latrans*, harmonic mean, minimum convex polygon, territory

Home range has been defined as the area an animal traverses in its normal activities, where it performs behaviors such as feeding, resting, mating, and rearing young. The concept and description of a home range allow better understanding of animal distribution and movements over the landscape (Burt 1943). Interest in animal movements has resulted in a plethora of methods to identify areas of concentrated use within a home range (Samuel et al. 1985). Some authors have provided reviews and discussions of home range estimators (Worton 1987), computer-aided simulations (Bekoff and Mech 1984, Boulanger and White 1990), reviews of current software (Larkin and Halkin 1994), and discussions of statistical considerations (Swihart and Slade 1985, Andersen and Rongstad 1989, Gese et al. 1990), but computer simulations are insufficient

for examining the biological relevance of mathematical representations of biological phenomena.

Because divining the biological meaning of spatial information is the ultimate purpose of home range estimators, animal behavior, not just mathematical or statistical considerations, should determine whether a particular home range estimator should be used. Simulations may indicate that home range estimators are only general measures of animal activity (Boulanger and White 1990), but identification of behavioral correlates within an estimated home range is the ultimate test of an estimator's usefulness.

Coyote (*Canis latrans*) space use has been a subject of much discussion (Laundré and Keller 1984). Coyotes are territorial and use the periphery of their territories differentially for scent-marking and

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howling (Barrette and Messier 1980; Bowen and Cowan 1980; Gese and Ruff 1997, 1998), but coyotes also make frequent forays out of their territories, sometimes into the territories of other coyotes (Shivik et al. 1996). Therefore, space use for coyotes is likely to be non-normally distributed. Land area that is visited infrequently is likely to be larger than that used regularly (home range) or defended (territory). Boundaries of calculated home range contours should have some relevance to actual home range or territory to be of most use to biologists.

Other authors have suggested the biological significance of particular home range contours, but without clear biological justification and no methodological consistency. For example, Shivik et al. (1996) defined a core area as the 64% adaptive kernel estimate, but Springer (1982) defined a core area using the minimum area method (Harvey and Barbour 1965), both with reasonable mathematical justification. Mills and Knowlton (1991) considered core areas to be equivalent to territories. The matter deserves more study. Clearly, a territory should not be confused with a home range or home range calculation (Burt 1943), but little study of the biological significance of home range estimates has been reported. Given the advances in probabilistic analysis of animal space use, our objective in this paper was to determine how well 3 widely available home range estimators identify a coyote territory and which use-contour best constitutes or defines a territory.

Methods

The large number of existing computer programs and estimation procedures precluded a thorough comparison of every method and program, but we considered the minimum convex polygon (Mohr 1947), harmonic mean (Dixon and Chapman 1980), and adaptive kernel (Worton 1989) estimators to be among the more widely used and thus most appropriately examined methods. We used the computer program CALHOME (Kie et al. 1994) for all home range analyses.

Locational data in our analyses were from direct observation of coyotes in the Lamar River Valley, Yellowstone National Park, Wyoming, during 1991–1993. Behavioral data and observation methods are addressed in detail elsewhere (Gese et al. 1996a,b,c; Gese and Ruff 1997). We randomly picked a coyote to observe and used focal animal sampling (Lehner 1979) to record the daily loca-

tions and behaviors (e.g., hunting, resting, scent-marking, traveling) of each coyote. We recorded most observations during diurnal hours (usually between 07:00 and 20:00 h), but we also collected nocturnal observations using an 11-power night-vision scope. We plotted locations to the nearest 10 m on 1:24,000 United States Geological Survey topographic maps using Universal Transverse Mercator grid system coordinates.

We used recorded locations to construct annual spatial data sets of all members of the Fossil Forest coyote pack for 1991–1993 and the Soda Butte pack for 1991–1992. In the Fossil Forest pack, there were no areas of dense vegetation where behaviors could not be observed and we visually located coyotes during 97% of attempts. In the Soda Butte pack, vegetation and topography blocked direct observation in some areas and we located coyotes during 56% of attempts, but territorial boundaries were well defined and observable. We analyzed a set of locations where each coyote performed particular behaviors (e.g., resting, traveling, scent-marking); the data set included positions taken after coyotes moved, but also included repeated coordinates at locations where coyotes rested or fed.

Coyotes use scent-marking to delineate and defend an area (Peters and Mech 1975, Gese and Ruff 1997) and thus it defines a territory (Drickamer and Vessey 1986). We mapped annual coyote territories using peripheral scent-marking behaviors of all pack members within each observational year. We imported all data points, territories, and home range contours into ATLAS GIS (Version 2.0, Strategic Mapping, Santa Clara, Calif.) for spatial analysis.

We performed spatial analyses using 2 observational units, individual coyotes within year or pack within year. Because home range estimations for coyotes are usually based on behavior of individuals and not lumped into a "pack" estimation, it was necessary to perform analyses with individual coyotes as the observational unit. Within packs, however, there is an inherent lack of independence when examining territorial use by packmates. To allow inference to other packs in valleys such as Lamar, we used the pack as the observational unit in a secondary analysis. That is, each coyote's space use was considered a sample in the estimation of a pack's annual space use.

To compare estimated home ranges to mapped territories, we calculated each pack member's home range with the minimum convex polygon
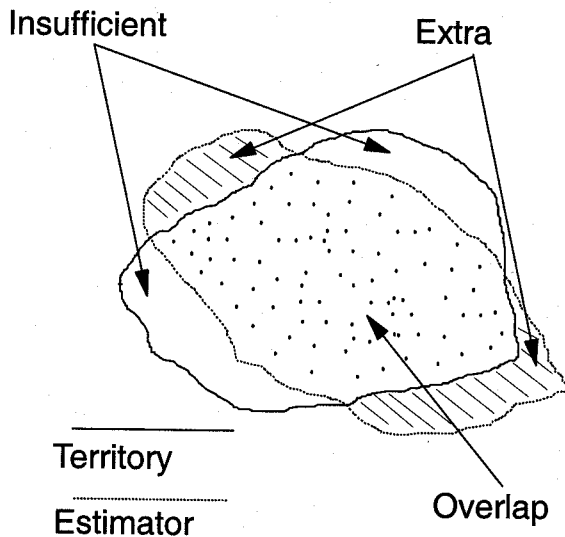
Figure 1. Graphic representation of comparison of home range estimate and territory. An index of fit was calculated by subtracting the area of the extra and insufficient polygons from the area of overlap, weighted by the absolute size of the territory and estimate.

(MCP), harmonic mean (HM), and adaptive kernel (AK) methods in CALHOME. We first calculated spatial contours for each home range estimator (e.g., 80%, 85%, 90%) to determine the contour (within each estimation method) that best defined a territory. Because we required a quantitative measure of fit between actual territory and estimated home range (measured in m^2), we devised an index to identify how well estimated home ranges from each coyote corresponded with that year's territory. The fitness index was simply a value of overlap of the estimated home range over the actual territory weighted by size of the territory and estimate (Figure 1):

Home Range Estimate of Territorial "Fit" =
$$\{1 + [Ov - (Ex + In) / (Ter + Est)]\} / 1.5 ,$$

where Ov = amount of overlap between the estimated home range and actual territory; Ex = the extra space enclosed by the estimate, but not actually part of the territory; In = insufficient area covered by the territory, but not by the estimator; Ter = territory area; Est = estimator area (Figure 1). The index has the property that as an estimate more correctly defines a territory (by increasing overlap while decreasing extra and insufficient area), the index approaches one; when there is no overlap, the index is 0; and when there is 50% overlap, the index is 0.5. Because fit is penalized by extra and insufficient area, the index approaches 0 when

territory area is greatly over- or under-estimated.

We attempted to perform 2 tasks with these analyses: 1) determine which home range contour (within each method) best fits the territory and 2) determine which home range estimator (at its best contour) best fits the territory. Using individual pack members as sample units, we determined the best contour for each home range estimator by computing the index of fit for each contour iteratively until we identified the contour with the greatest index of fit. Because the study was observational, we did not analyze data in an hypothesis testing framework (Johnson 1999); we summarize conclusions based on means and interpret results relative to associated measures of variability.

Results

We observed coyotes from 27 January 1991 to 30 June 1993, excluding August and September observations (when vegetation was too high and dense to allow reliable observation). In the analysis based on 15 individual coyotes within each year, larger contour levels were indicative of territory (Table 1). Estimated home range contours that best fit territories were the 94% (SE = 0.87%), 93% (SE = 1.11%), and 96% (SE = 0.84%) for the AK, HM, and MCP, respectively. Although the MCP method usually described the territory best (8 of 15 observations), within each method there was no wide difference in adequacy of the best home range contour to define a territory; AK fit was 0.68 (SE = 0.02), HM fit was 0.70, (SE = 0.03), and MCP fit was 0.74 (SE = 0.02). Overall, the home range estimators described the Fossil Forest territory (fit = 0.73, SE = 0.02) slightly better than the Soda Butte territory (fit = 0.67, SE = 0.02).

In analyses using packs as the sample unit, we also did not observe a dramatic difference in the home range contours that best described a territory (AK = 94%, SE = 1.21%; HM 94%, SE = 1.45%; MCP = 96% SE = 0.73%), nor was there a large difference between fit of the best contours of each method (AK = 0.67, SE = 0.03; HM = 0.69, SE = 0.04; MCP = 0.74, SE = 0.02), although the MCP method estimate usually fit the actual territory best (Table 2).

Discussion

Using either individual coyotes or packs as observational units produced very similar results, suggesting the correspondence of space use among all

Table 1. Data from home range analysis of coyotes from Yellowstone National Park, 1991–1993.[a]

COYOTE	PACK	n	YEAR	SEX	STATUS	Home Range Estimator					
						AK	AKF	HM	HMF	MCP	MCPF
369	FF	326	91	M	PUP	89	0.751	89	0.854	90	0.794
920	FF	291	91	F	ALPHA	95	0.729	92	0.785	95	0.735
AMF	FF	288	91	M	ALPHA	89.5	0.794	93	0.813	99	0.871
379	FF	240	92	M	BETA	96	0.613	97	0.722	99	0.762
369	FF	423	92	M	BETA	90	0.715	85	0.783	93	0.769
920	FF	679	92	F	ALPHA	93	0.687	94	0.770	95	0.764
AMF	FF	409	92	M	ALPHA	94	0.697	95	0.739	100	0.794
AMF	FF	257	93	M	ALPHA	98	0.572	99	0.673	95	0.801
920	FF	417	93	F	ALPHA	95	0.531	99	0.475	92.5	0.704
MSB	SB	277	91	M	ALPHA	90	0.642	92	0.606	92	0.702
958	SB	272	91	F	ALPHA	93	0.657	90	0.699	98	0.673
MSB	SB	418	92	M	ALPHA	93	0.655	91.5	0.621	98	0.755
140	SB	165	92	M	BETA	97	0.666	96	0.585	94	0.638
080	SB	206	92	M	BETA	100	0.654	100	0.652	100	0.566
958	SB	468	92	F	ALPHA	97.5	0.791	89	0.653	99	0.807

[a] HM = Harmonic mean, best contour; HMF = Harmonic mean, fitness at best contour; AK = Adaptive Kernel, best contour; AKF = Adaptive Kernel, fitness at best contour; MCP = Minimum Convex Polygon, best contour; MCPF = Minimum Convex Polygon, fitness at best contour.

pack members. Differences in space use between the 2 packs were minor, also suggesting that our results are relevant to other researchers working in areas similar to the Lamar Valley, but it is possible that land-use patterns may be more variable between packs (especially in other areas) than between coyotes within a pack. Furthermore, movements in the Soda Butte pack were not described as thoroughly as those in the Fossil Forest pack due to reduced observability of Soda Butte coyotes, and possible bias in observations is impossible to identify. Equivalent home range contours were identified as best, however, suggesting robustness of the estimators to differential spatial observability. The effect of differential spatial observability is relevant to most studies because habitat and topographical features of most study areas may often contain areas which block direct or radio observation and thus could influence analysis of space use.

It is not surprising that results of the harmonic mean, being a special case of kernel estimator, were equivalent to the adaptive kernel (Larkin and Halkin 1994). However, the minimum convex polygon, which is mathematically and intuitively the simplest method, performed well as an estimator of coyote territory. Although methods such as the AK

Table 2. Data from home range analysis of coyotes from the Fossil Forest Pack (FF) and Soda Butte Pack (SB), Lamar Valley, Yellowstone National Park, Wyoming 1991–1993. Fitness values index fit of home range contours to actual pack territories and contour values are percentage contours of each home range estimator that best fit the pack territory.[a]

PACK	YEAR	n	Home Range Estimator[b]		
			AK	HM	MCP
Fitness					
FF	91	3	0.758 (0.019)	0.817 (0.020)	0.800 (0.039)
FF	92	4	0.678 (0.022)	0.754 (0.014)	0.772 (0.007)
FF	93	2	0.552 (0.020)	0.574 (0.099)	0.753 (0.049)
SB	91	2	0.650 (0.008)	0.653 (0.047)	0.688 (0.014)
SB	92	4	0.692 (0.033)	0.628 (0.016)	0.692 (0.055)
Contour					
FF	91	3	91.17 (1.92)	91.33 (1.20)	94.67 (2.60)
FF	92	4	93.25 (1.25)	92.75 (2.66)	96.75 (1.65)
FF	93	2	96.50 (1.50)	99.00 (0.00)	93.75 (1.25)
SB	91	2	91.50 (1.50)	91.00 (1.00)	95.00 (3.00)
SB	92	4	96.88 (1.45)	94.13 (2.44)	97.75 (1.32)

[a] AK = Adaptive Kernel; HM = Harmonic mean; MCP = Minimum Convex Polygon.
[b] Numbers in parentheses = SE.

and HM were devised because the MCP could contain areas of land that animals did not visit (Harris et al. 1990), these newer estimators did not solve this problem and still overestimated space use (Figure 2). We do not conclude that methods other than the MCP are not useful measures of animal activity, but that the MCP is intuitively a simpler estimator with fewer statistical assumptions and appears to have at least as much biological meaning, in terms of coyote territory, as the probabilistic models. We limit our inferences to coyotes in the Lamar Valley, however, and note that movements of other coyotes, especially nonterritorial animals, coyotes with different-sized packs, or coyotes existing in different topography may be still better described using the probabilistic models.
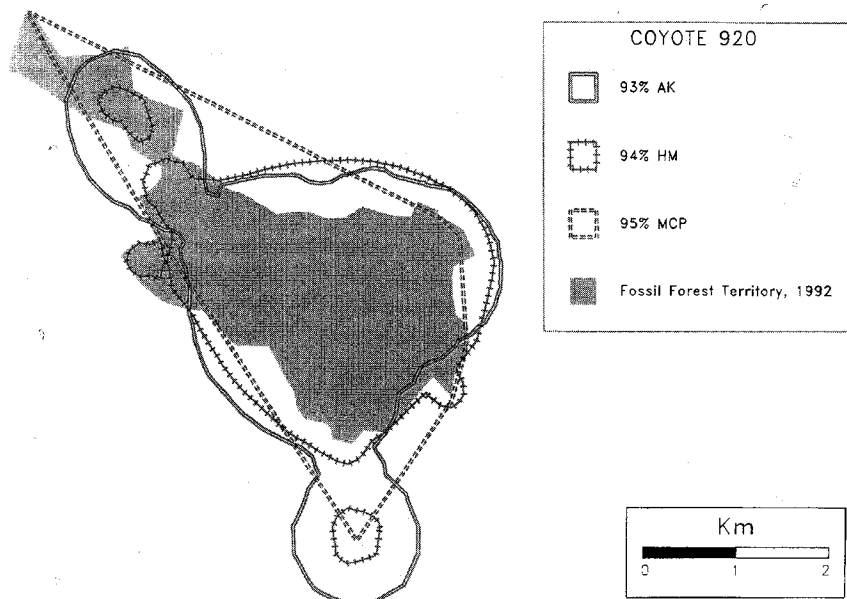

Figure 2. Best fitting contours from the harmonic mean (HM), adaptive kernel (AK), and minimum convex polygon (MCP) overlapped with the territory of alpha female coyote 920, Yellowstone National Park, 1992. For a graphic representation of home range and actual territory, this animal was chosen randomly from the 9 coyotes that were analyzed. HM fit index =0.770, AK fit index=0.687, MCP fit index=0.764.

Use of a particular home range estimator should be based on mathematical constructs but also incorporate biological and topographical understanding gained from study of animals; mathematical simulations are extremely useful in the study of behavior, but we caution that without correlation to biological reality, the usefulness of simulations for describing animal behavior is limited. Wildlife managers are concerned largely with describing the 2-dimensional area of animal use, not necessarily only areas of great use within home ranges. To determine upper limits of species density and area required for a particular species, boundaries of space use are often of greatest concern. Each of the 3 methods examined has particular strengths and weaknesses (Harris et al. 1990), and based on our results, none of the estimators provided a perfect fit to coyote territory. As mathematical descriptors are refined, it will continue to be important to use both computer simulation and actual biological data to validate and understand home range estimators.

We used direct observations, rather than radiotelemetry data. Telemetry is certainly the more common method of recording spatial data for coyotes, but our method allowed a better analysis of actual home range estimator performance because of the absence of telemetry error. This strengthens our conclusions, but may limit inference to radiotelemetry studies based on the effects of telemetry error on home range estimators (White and Garrott 1986, Mills and Knowlton 1991) until the relatively small errors produced by GPS equipment are implemented in most wildlife monitors.

Although other authors have excluded the outer 5% of points from MCP home range calculations, admitting that this practice has "no specific biological basis" other than to exclude sallies from frequently used areas (Bowen 1982), we note here that excluding outer points with the MCP and other estimators does indeed have a biological basis for coyotes. Furthermore, contours of home range estimators should be used with some biological understanding, and our data suggest that for coyotes in the Lamar Valley, the 96% MCP is appropriately sized relative to an actual territory. We cannot conclude that the 96% MCP is the best estimator and promote its use for all coyotes in all areas, but we hope that replicates of this study will give biologists strong biological justification for use of a particular home range estimator. Defining arbitrary

contours (Springer 1982, Shivik et al. 1996) or core areas as territories (Mills and Knowlton 1991) may be problematic. For instance, areas of great use may actually occur outside of the actual marked territory (Figure 2), but if researchers are concerned with coyote territory and have sufficient sample sizes in areas similar to our study area, the MCP is an appropriate method to delineate coyote use areas.

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