Snow-tracking versus radiotelemetry for predicting wolf-environment relationships in the Rocky Mountains of Canada

Shelley M. Alexander, Paul C. Paquet, Travis B. Logan, and D. Joanne Saher

Abstract We tested the efficacy of a snow-tracking-based model for predicting wolf (*Canis lupus*) distribution and environmental relationships, using n independent radiotelemetry data dataset. We documented tracks in snow on highway rights-of-way and adjacent transects in the central Rocky Mountains of Alberta, Canada between November and March, 1997–2000. Radiotelemetry data (ground and aerial) were collected in the same region for 2 wolf packs between 1991–1993. We assessed the relationship between wolf track data and topographic, vegetative, and prey metrics, using a Geographic Information System (GIS), logistic regression, and Akaike's Information Criterion (AIC). We transformed our optimal regression model into a probability surface in GIS and verified that surface using radiotelemetry data and a Receiver Operating Characteristic (ROC) curve. The optimal model showed that wolf presences were positively related to wetness (mature, possibly more complex forest), and elk (*Cervus elaphus*), and deer (*Odocoileus* sp.) track density and negatively associated with terrain ruggedness and open canopy. The ROC curve indicated that the track-based model was robust (AUC=0.78). We concluded that track data provide a reliable, cost-effective approach for determining distribution and predicting wolf–environmental relationships in mountainous regions.

Key words AIC, Akaike's Information Criterion, *Canis lupus*, Canadian Rocky Mountains, Geographic Information System, GIS, habitat associations, logistic regression, non-invasive sampling, tracking data, wolves

Knowledge of the area in which a species occurs and the environmental resources upon which it depends is fundamental for implementation of successful conservation strategies. Species distribution and resource selection models use a multitude of sampling and statistical analysis techniques to derive these species–environment relationships (Corsi et al. 2000). Among the approaches used to acquire animal locations essential to such models, radiotelemetry is one of the most common. The method, however, is invasive because it requires immobilizing and handling study animals. Moreover, some of the most effective methods used to capture wild animals are controversial and, in

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specific areas, banned from use (Friend et al. 1994, Shivik et al. 2000, Way et al. 2002). Improved capture methods (i.e., net guns and rubber-jawed leghold traps) have reduced injury and handling trauma, but the physiological and behavioral effects on individual animals remain poorly understood (White et al. 1991, Murray and Fuller 2000). Finally, telemetry can be time-consuming, expensive, and prone to location error (Weckerly and Ricca 2000).

Although not a substitute for telemetry research, non-invasive monitoring (e.g. track surveys and fecal, hair, and chemical assays) is gaining popularity in wildlife research and conservation because of fewer associated negative effects (Woods et al. 1999, Millspaugh et al. 2001, Schauster et al. 2002, Darimont et al. 2004). Snow-tracking surveys have proven to be a practical method to measure presence and distribution and, in some cases, abundance of carnivores (Oehler and Litvaitis 1996, Ciucci et al. 2003). Track-based data also have been suggested suitable for predicting patterns of biological diversity, identifying areas of conservation significance, and assessing habitat potential of unstudied sites (Corsi et al. 2000, Lenton et al. 2000, Debinski et al. 2002).

We are aware of no studies, however, that have examined the efficacy of tracking versus radiotelemetry in elucidating the species–environment relationships of large carnivores such as wolves (*Canis lupus*). Hence, we used track data to develop a predictive model for wolves and tested it against independent radiotelemetry data for the same region. If robust, this non-invasive tracking approach could make predictive modeling and long-term monitoring of wolf distribution and environment relationships more feasible for management agencies, which should assist in effective conservation decision-making in the region.

Study area

We conducted research in the Kananaskis River and Spray River drainages, Kananaskis Country, Alberta, approximately 110 km west of Calgary. The landscape was typical of the Canadian Rocky Mountain Cordillera, characterized by rugged mountainous terrain, steep valleys, and narrow (2–5-km), flat valley bottoms. Elevation, aspect, slope, soil, and local climate determined vegetation communities in the study area, which could be classified into 3 broad ecoregions: montane (1,300–1,600 m), subalpine (1,600–2,300 m), and alpine (2,300 + m). Average annual precipitation ranged from 455 mm in montane regions to 763 mm in the upper subalpine (Alexander et al. 2004). Monthly precipitation peaked in May–July, and snow thickness maximums occurred in November–December and March–April. Large predators in the region included gray wolf, coyote (*C. latrans*), grizzly bear (*Ursus arctos*), black bear (*U. americanus*), cougar (*Puma concolor*), lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), and wolverine (*Gulo gulo*). Prey species included moose (*Alces alces*), elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), mountain goat (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*).

Methods

Transect and road-track data (1997–2000)

Winter tracking depended upon snowfall and involved monitoring road rights-of-way and fixed transects for wildlife tracks (Alexander et al. 2004). We collected track data for 13 mammal species (Alexander et al. 2004) along 4 highways of varying traffic volume, from November to April (1997–1998 through 1999–2000). We adapted tracking methods from Van Dyke et al. (1986), Thompson et al. (1988), Beier and Cunningham (1996), and Oehler and Litvaitis (1996). Here we focus only on wolf track data collected along Highway 40 (Hwy 40) and the Smith-Dorrien Trail in Kananaskis Country.

We surveyed roads from vehicles approximately 24 hours after every snowfall, recording road crossings of wolves while driving 15–20 km/hour. We surveyed every 3–4 days thereafter, until the next snowfall. Road-crossing data were georeferenced with a hand-held Garmin GPS (location error ± 50–130 m). We surveyed 10 1-km transects fixed perpendicular to each road on foot between 24 and 120 hours after snowfall, following each road survey. We required 120 hours to complete all transect surveys in the larger study (Alexander 2001). We georeferenced transect data by assigning each 50-m transect interval a UTM, using a backpack Trimble Pathfinder GPS (Cansel Survey Equipment, Calgary, Alberta) and differentially corrected data down to within 1-m accuracy. Except for rare occasions, wolf movements were perpendicular to transects and did not indicate that animals were weaving up, paralleling, or crossing any single transect multiple times in one survey period.

Telemetry data (1991–1994)

Over a 3-year period, we monitored 2 radiocollared wolf packs whose home ranges overlapped with our tracking (road and transect) study area. We used daily ground telemetry surveys stratified over 24 hours and conducted aerial surveys when we were unable to detect wolves for more than 3 days. We confirmed all telemetry locations by finding wolf tracks on the ground (Paquet et al. 1996). Although it reduced our dataset, we analyzed only those locations that occurred within 1 km of the telemetry observer. Paquet et al. (19963) determined that locations at this distance had a corresponding error of ±50 m, which was less than the minimum vegetation polygon diameter (determined using GIS) and thus reliable for habitat modeling. Combining ground and aerial data that met the previous criteria, we recorded 331 telemetry locations that occurred within the spatial extent of our road- and transect-tracking study site.

Derivation of spatial data: wolf presence and predictive attributes

Using species presence–absence data from track surveys and independent ecological metrics (e.g., slope, aspect, elevation, etc.), we developed a predictive logistic regression model, which we transformed into a wolf probability surface (Figure 1).

Our dependent variable was binary; presence data were track locations, and pseudo-absence data were randomly sampled point locations. In most cases absolute absence was unknown (Garshelis 2000), so we referred to these points as pseudo-absence data. To select pseudo-absence points, we developed an analytical frame that included all areas within ±130 m of roads and 60 m of each transect line; this reflected the respective GPS error. We extracted 1,000 "pseudo-absence" points were from within this frame using ArcView, Animal Movement (Hooge and Eichenlaub 1997) and removed those overlapping with known presence. The specified analytical frame reduced the effects of framing bias because it narrowed the possible area from which to draw absence points to an area that reflected, with as much accuracy as possible, sites that were actually surveyed (Verbyla and Chang 1994).

Independent variables included measures of topography, vegetation, and prey-species track density. Topographic metrics consisted of elevation, terrain ruggedness index (TRI), and measures of aspect (northness and eastness). The terrain ruggedness index measures variation in elevation within a 3x3 neighborhood, derived by the equation: $TRI = [\Sigma(X_{ij} - X_{00})^2]^{1/2}$, where X_{ij} = elevation of each neighbor pixel to the center pixel, X_{00} (Riley et al. 1999). Northness and eastness were derived using cosine and sine transformations of aspect, respectively.

Vegetation metrics consisted of greenness, which was proportionate to green biomass at a specific time (Crist and Ciccone 1984, Jensen 1996, Mace et al. 1999) and wetness, which correlated strongly with vegetation structure and soil moisture (Cohen et al. 1995, Todd et al. 1998, Hansen et al. 2001). Greenness and wetness were derived using a Tasseled Cap Transformation (Jensen 1996) of Landsat 7 Enhanced Thematic Mapper (ETM) imagery (United States Geologic Survey, http://www.usgs.gov/). A Normalized Difference Vegetation Index (NDVI) also was derived from Landsat imagery (Jensen 1996) for comparison as a vegetation productivity surrogate. We developed a canopy closure metric (CanopyDens) that classified the landscape based on proximity to closed canopy. In the latter case, we used a circular moving window on a polygon coverage showing forested and nonforested habitat and quantified the percent of forest cover within a 500-m radius. This approach addresses problems that arise when observations occur along forest edges (i.e., the fuzzy versus discrete boundary problem in GIS.)

Lastly, we created prey density layers for elk (E.dens) and deer (D.dens) using track data collected simultaneously with wolf data (Alexander 2001). We applied a kernel density estimator (a 3x3 moving window) to point track counts, which resulted in an image that showed generalized track density of elk and deer.

Spatial data analysis

We extracted attribute values for all independent variables associated with track-based presence and pseudo-absence, using ArcView, GetGrid. We tested independent variables for multicollinearity using Pearson's correlation coefficient (Tabachnik and Fidell 2001). When pairs of variables exhibited correlation values above 0.7, we removed the variable with the lowest predictive power, determined with a univariate logistic model (Tabachnik and Fidell 2001). We excluded slope and NDVI because of high correlation with elevation and greenness, respectively.

We analyzed presence/pseudo-absence data using binary logistic regression (Glenz et al. 2001,

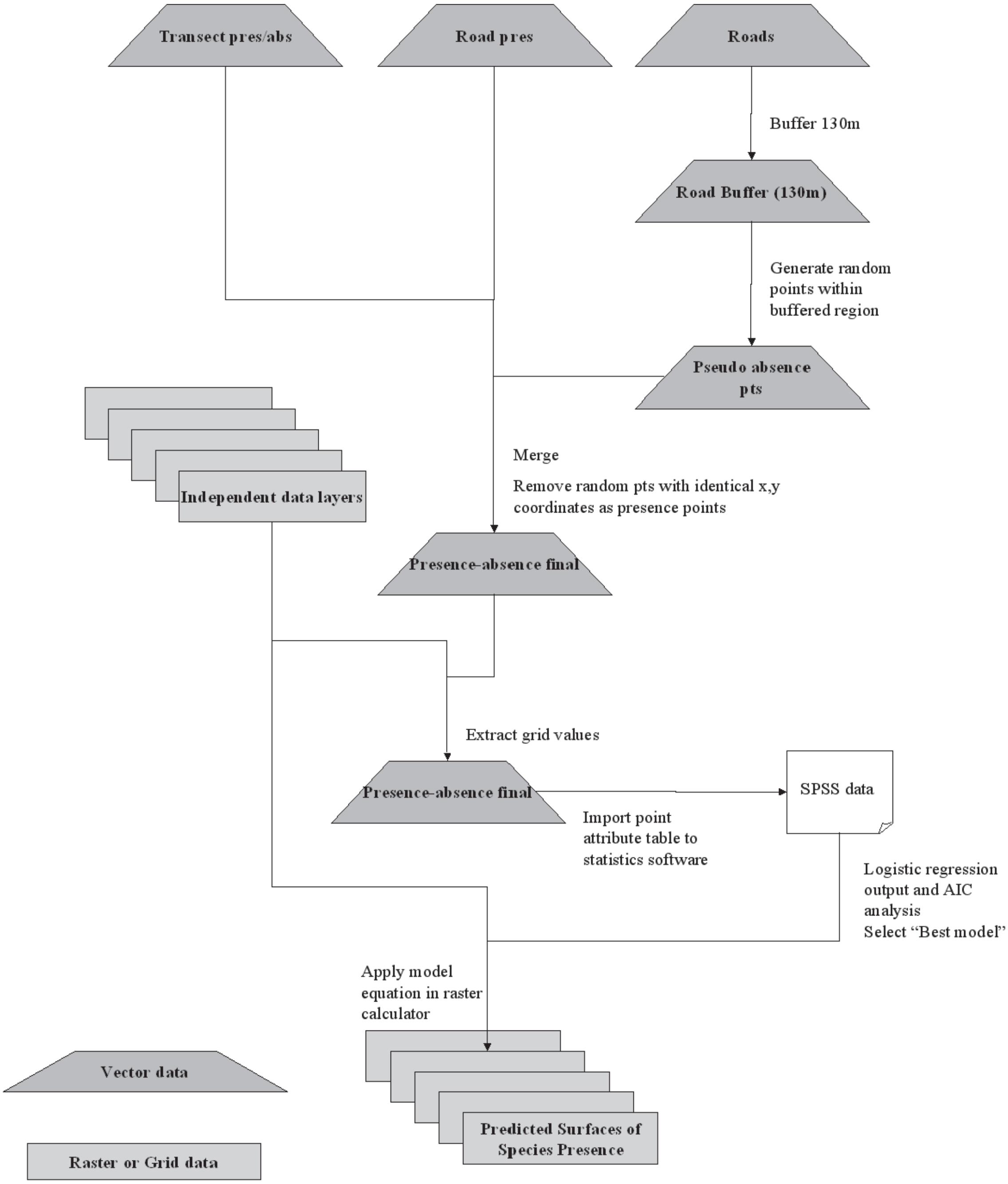

Figure 1. Flow chart outlining steps in wolf habitat model creation, Kananaskis Country, Alberta, Canada, 1997–2000.

Manly et al. 2002), which is one of the most common statistical techniques currently used in habitat modeling (Mace et al. 1996, Boyce and McDonald 1999). We excluded variables from further analysis when $p > 0.2$ (Hosmer and Lemeshow 2000) and used AIC model selection techniques (Anderson et al. 2000, Burnham and Anderson 2002) to rank a suite of 30 candidate models including univariate and multivariate combinations of variables. We ranked models based on the difference in the AIC_c (AIC corrected for small sample size) values from the minimum AIC_c, or ΔAIC_c. We used Akaike weights (w_i) to assess the strength of evidence that any particular model was the best model in our set

Table 1. Akaike's Information Criterion (AIC) model selection results (Top 3 ranked models of 30 candidates), Kananaskis Country, Alberta, Canada, 1997–2000

K	AICc	Δ I	*w*	Rank	Variables in the model					
6	1,327.15	0.00	0.485	1	TRI	CanopyDens	Wet	E.dens	D.dens	
7	1,328.88	1.73	0.204	2	TRI	CanopyDens	Wet	Northness	E.dens	D.dens
5	1,329.19	2.04	0.174	3	TRI	CanopyDens	Wet	E.dens		

of candidate models, given the data (Anderson et al. 2000). Finally, we created a landscape-scale wolf-probability surface by extrapolating the optimal model across Kananaskis using ArcView, raster calculator, thus incorporating sites not initially surveyed.

Verification of the track-based predictive model

We verified the track-based probability surface (i.e., the spatial extension of the optimal model) using independent radiotelemetry data in a Receiver Operator Characteristic (ROC) curve calculation. The ROC curve assesses model discrimination over the entire range of probability thresholds ranging from 0–1 and presents results as an area under curve (AUC) score (Fielding and Bell 1997, Pearce and Ferrier 2000). We extracted values from the track-based predictive surface that corresponded with a known wolf telemetry locations and 1,000 randomly selected pseudo-absence points and then calculated the ROC curve and AUC value. Pseudo-absence telemetry points were selected from a home range area, defined using telemetry presence points and an adaptive kernel estimator in ArcView, Animal Movement (Hooge and Eichenlaub 1997).

Results

Logistic regression and AIC selection

Our primary objective was to examine the predictive modeling potential of one method (tracking) with another (telemetry). As such, we were less concerned with the biological explanation of variables selected in the optimal model. However, the intuitive and biological correctness of the model was critical to its validity, and we discuss our results briefly for that reason.

Our optimal track-based model showed that wolf presence was a function of terrain ruggedness, vegetation cover, wetness, and prey density (Table 1) as follows:

$$\mathrm{Ln}[p / (1 - p)] = (-1.64 - 0.016\mathrm{TRI} - 1.307\mathrm{CoverDens} + 0.048\mathrm{Wet} + 0.032\mathrm{E.dens} + 0.02\mathrm{D.dens}).$$

The above equation shows that wolf presence was negatively associated with terrain ruggedness (TRI) and the percent of forest cover within 500 m (CoverDens) and positively associated with wetness (Wet) and the density of elk (E.dens) and deer (D.dens). The above model was 2.4 times better at explaining wolf presence than the second-best model, which included all variables above in addition to northness (negative relationship) (Table I). The third-optimal model replicated the top model except that deer were not an important determinant of wolf presence.

Model comparison

We first inspected our predictive regression model (above) for intuitive integrity, a fundamental component of model evaluation (Burnham and Anderson 2002). Based on our collective knowledge of wolf behavior in the region, we concurred that the predictions were highly plausible. In addition, a visual examination of the spatial model showed that telemetry data (presence-only displayed) were consistent with high wolf-probability sites.

Our quantitative evaluation (ROC) showed strong model discrimination (Figure 2). The ROC curve (Figure 2) showed a large amount of separation from the 1:1 line for most threshold values, indicating model performance much better than chance. The AUC calculation confirmed that the tracking-based model performed well when compared with independent telemetry predictions (AUC=0.78).

Discussion

The model derived from snow-tracking data showed that wolves had a high likelihood of using flat areas (i.e., low TRI) with less dense, older, and

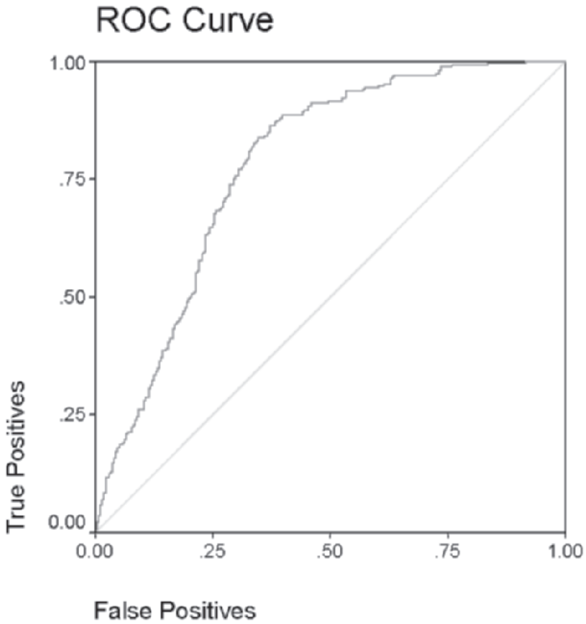

Figure 2. ROC curve comparing telemetry presence–absence locations with tracking model predictions. The 1:1 line represents very poor model discrimination where discrimination is no better than chance. Our model showed (AUC = 0.78), which indicated that model correctly discriminates between positive and negative cases 78% of the time, Kananaskis Country, Alberta, Canada, 1997–2000.

perhaps more complex forest types (i.e., higher wetness index) and a higher probability of encountering elk and deer (i.e., track density).

The use of more open forest (i.e., low-canopy cover) with low topographic complexity can facilitate movement for wolves by reducing the energetic expenditure associated with travel (Paquet 1993). The selection for wetness may indicate preference for structurally complex or older-growth forests and may increase the encounter rate with prey species that select more complex vegetation types for bedding, browse, or concealment of young. Wetness also can relate to greater soil moisture content or coarse woody debris (CWD) on the forest floor, which would not be consistent with easier travel. However, because our second model indicated a preference for more southern aspects, we suggest that wetness in the present case relates more to forest maturity or stand complexity than to moisture or CWD; southern slopes in this region are drier and characterized by more open forest types. In the central Canadian Rocky Mountains, elk and deer often concentrate in vegetated valley bottoms as opposed to steeper, more rugged slopes and ridges, and may choose more complex forest types as noted above (Alexander et al. 2004). Combined, the previous results suggest that wolves may be optimizing fitness by reducing travel costs, while maintaining better potential for prey encounters.

In addition, avoidance of rugged terrain by wolves could be a key factor in niche partitioning of habitat from cougars (*Puma concolor*) (Paquet et al. 1996, Carroll et al. 2001). For example, Logan (2003) found that cougars selected for high terrain ruggednessI (TRI). This can afford cougars the opportunity to stalk and ambush elk and deer and access to other prey species such as sheep. Partitioning of this type may reduce inter-specific competition, making coexistence more probable (Voeten and Prins 1999, Kingston et al. 2000, Loreau and Hector 2001).

Our winter tracking-based model showed good concordance with the telemetry-based presence–absence data. The AUC value indicated that our tracking model discriminated telemetry presence–absence correctly 78% of the time, which was acceptable for this type of spatial modeling. Radiotelemetry data represented annual distribution, whereas the snow-tracking data were limited to winter and may have failed to capture seasonal variation in wolf–environment relationships. Notably, however, winter movements of wolves in the central Rockies follow a downward migration to lower elevations due to constraints imposed by snow (Paquet et al. 1996). In addition, we have observed wolves to use the same paths in valley bottoms in all seasons, although vertical movements expand and occur less often in valley bottoms during summer (Paquet et al. 1996). Thus, we contend that movement detected in winter should represent the maximum encounter rate (i.e., in frequency and spatial extent) and adequately encompass summer movement. More importantly, constraints imposed on movement by snow may suggest that sites selected for movement in winter are critical in order to reduce the energetic cost of movement to wolves.

Although snow-tracking cannot provide all the information available from radiotelemetry, we showed that a track-based predictive model has high efficacy relative to telemetry for species–environment modeling. Telemetry, likewise, is not a complete substitute for snow-tracking. The appropriateness of the method depends on the species being studied, research questions, geographic location, physiography of the study area, funding, and logistics. Moreover, snow-tracking and radiotelemetry can be combined, which diminishes the inherent weaknesses of both methods.

Our results also suggest that some predictive models may be reliably extrapolated beyond the area of survey (i.e., beyond the exact transects and ±130 m of roads). We do not suggest extending the predictive model to less topographically complex terrain but believe it may be reliable to generalize to other study areas in the Rocky Mountains, within reason.

Lastly, as many remnant populations of wolves now exist only in more rugged mountain terrain (in Canada, United States, and internationally), we contend that tracking-based species–environment models may be a highly reliable method of inventory where funding is limited but surveys necessary.

Management implications

We showed that a landscape probability model developed using track data was highly consistent with telemetry data predictions. Thus, for specific research objectives, such as modeling wolf–environment relationships in mountainous terrain, locational data from non-invasive snow-tracking could be reliably substituted for radiotelemetry data. The efficacy of our model supports continued use, improvement, and expansion of such non-invasive techniques. Snow-tracking, however, cannot replace telemetry, which provides information about dispersal, individual identity, and social affiliations. However, funding for large-carnivore research increasingly is difficult to attain, while the need for research and conservation is more pressing than ever. Tracking can provide a solution to this situation; it is a cost-effective, reliable method to conduct long-term surveys of wolf distribution and environmental relationships, which, used appropriately, should foster ecologically relevant management and conservation decisions.

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