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Source: Wildlife Biology, 20(1) : 19-26

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.12100

Wildlife Biology 20: 19–26, 2014
doi: 10.2981/wlb.12100

Subject Editor: Andraes Zedrosser. Accepted 26 August 2013

Common biases in density estimation based on home range overlap with reference to pumas in Patagonia

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Density estimates are critical to proper population management and conservation, yet difficult to obtain for many wide-ranging or cryptic species. One proven method used to quantify carnivore density, especially species difficult to individually identify from photos taken by camera traps, utilizes overlapping home ranges of individual animals in the study area. This method, however, may be particularly prone to residency and extrapolation biases. Residency bias occurs when the reference area for the density estimate is incorrect, and extrapolation bias occurs when scaling a density to a different spatial extent than that of the study area upon which the estimate was based. We used a simulation approach based on GPS locations to diagnose potential biases in published densities of pumas *Puma concolor* from Patagonia, where Franklin et al. 1999 (Biol. Conserv. 90: 33–40) reported 'minimum' densities of 6 and 30 pumas per 100 km^2, and Elbroch and Wittmer 2012a (Mammal. Biol. 77: 377–384) reported densities of 3.4 pumas per 100 km^2. Using GPS data from the latter study we tested methods described in Franklin et al. (1999) and compared their outcomes. Our results showed that density estimates that do not account for residency bias resulted in severely inflated density estimates. Our findings also indicated that actual densities from Franklin et al. (1999) might have been an order of magnitude lower than reported, and therefore consistent with puma densities reported across the range of the species. Both studies introduced extrapolation bias by translating linearly their estimates to new spatial extents, although the magnitude of this bias was much less than that of residency bias. Our results underscore the need for rigorous accounting of residential space in estimating population density, and highlight the scale-dependency of density estimates.

If a central question of ecology is understanding the abundance and distribution of species (Andrewartha and Birch 1954), then a central challenge is measuring them. Estimating population density, defined as the number of individuals per unit area, is essential to creating viable conservation strategies for rare species, calculating harvest quotas for game species, determining the post-implementation effectiveness of management strategies, and in understanding complex inter- and intraspecific interactions including competition and predation (Gittleman et al. 2001, Sinclair et al. 2006, Mills 2007). Erroneous density estimates can lead to maladaptive management practices such as over-harvest or inadequate protection for small populations of animals.

Estimating population density is complicated by species-specific traits including life history and behavior. Among terrestrial mammals, males frequently have large home ranges that overlap several smaller home ranges of females (e.g. pumas *Puma concolor* in Logan and Sweanor 2010, American black bears *Ursus americanus* in Powell et al. 1997, Canada lynx *Lynx canadensis* in Vashon et al. 2008). Dispersers, defined as non-resident subadult individuals searching for areas in which to establish residence (Bowler and Benton 2005), can also bias density estimates during specific times of year (Börger et al. 2008). Density estimates may also be affected locally by behavioral changes associated with, for example, mate finding or anthropogenic disturbances such as hunting (Börger et al. 2008) or supplemental feeding (Smith 2001). Finally, geographically and temporally patchy resources can also result in disproportionate distributions of individuals across heterogeneous landscapes, and extremely abundant resources can degrade territoriality (exclusivity of home ranges) and contribute to species clumping (northern raccoons *Procyon lotor* in Prange et al. 2004, Eurasian lynx *Lynx lynx* in Herfindal et al. 2005, American black bears in Powell et al. 1997, brown bears *Ursus arctos* in McLoughlin et al. 2000).

The accuracy of density estimates also depends on researcher decisions, including the methods used to count animals in the field as well as the delineation of the area over which surveys are conducted. For example, density estimates may be biased by non-random sampling of individuals or areas (McLellan 1989, Blackburn and Gaston 1996, Smallwood and Schonewald 1998). Individual animals vary in their detection probabilities, and animals learn from

experience, changing their detection probabilities over the course of the study. For example, animals may learn to avoid specific trap configurations and so are only trapped once, or in opposite cases, some animals may learn that traps provide easy food rewards, and may be caught repeatedly over a short duration. Further, study areas are typically selected for species management, conservation, or other practical reasons such as accessibility, rather than at random, and this non-random selection process undermines the ability to generalize results. This is important because the geographic extent of a study matters, both in terms of the absolute numbers of animals to count, and in terms of the independence of density estimates with respect to study area.

Estimating population densities of carnivores is of particular interest due to their potential keystone ecological functions in natural systems (including direct predation and indirect effects that support biodiversity) and their wide-scale reliance on conservation strategies for population persistence (Creel et al. 2001, Hebblewhite et al. 2005, Soulé et al. 2005, Elbroch and Wittmer 2012b). Accurately measuring population densities of carnivores, however, poses great challenges, because carnivores learn quickly from experience (McLellan 1989), and are often cryptic and live at low densities in remote areas (Long et al. 2008). A widely used method to estimate carnivore densities is based on proportional residencies of individuals within the study area (McLellan 1989, Cooley et al. 2009, Elbroch and Wittmer 2012a), a calculation that accounts for individual animals as the proportion of their home ranges that intersect the study area boundaries (Kenward 1987, McLellan 1989). This method may be particularly attractive to researchers that already employ telemetry devices on study animals, those studying carnivores with uniform pelage, and those with the need and opportunity to collect additional data on individual and species ecology beyond that necessary for density estimation (e.g. movements and other behaviors).

Estimating densities from home range overlap, however, is prone to two forms of bias, even when species abundance in a given area is known with high confidence. Since density is the ratio of species abundance to unit area, and residency is established based on overlapping home ranges of non-transient individuals, 'residency bias' will be introduced to density estimation when the denominator in the density ratio is inaccurate. Radio-telemetry and GPS technology allow researchers to quantify the proportion of each marked animal's home range that should be included in the sampled spatial extent (Kenward 1987, McLellan 1989), an area that should also be large enough to include a suitable sample of individual home ranges. However, when the area of residency for individual animals is underestimated, the density will be over-estimated; if residency is overestimated, the reverse will be true. For example, an animal with a home range that overlaps 50% with the study area should be counted as 0.5 animals. If that animal is instead counted as 1 complete animal, we have miscalculated its area of residency by 50%. Such underestimation of residency causes density estimates to be positively biased (McLellan 1989).

Density estimates based on home range overlap are also prone to 'extrapolation bias'. Extrapolation bias occurs when a density estimate is extrapolated or projected to a spatial extent other than that of the study area for which it was estimated (i.e. researchers often report large mammal densities as the number of individual animals per 100 km^2 regardless of the size of sampling area) (Schonewald-Cox et al. 1991, Blackburn and Gaston 1996, Smallwood and Schonewald 1998, Smallwood and Smith 2001). Density estimates are site-specific and scale-specific (Smallwood and Schonewald 1998). Smaller study areas in relation to the spatial ecology of the target species generally capture small portions of individual animal home ranges and of the aggregate range of the local population (Maffei and Noss 2008). Should a small sample area be selected because animals are present, the area may then include a disproportionately high amount of high quality habitat, and in turn sustain higher animal densities. As the size of the sampled area increases, the proportion of lesser-quality habitat and less densely inhabited area is likely to increase in the sample, resulting in a lower overall density estimate (Blackburn and Gaston 1996). In order to identify and assess the degree of extrapolation bias inherent in the convention of reporting densities as animals per 100 km^2, in this paper, we discuss density estimates as 'unit densities', the number of animals per km^2.

Due to their large geographical range (Sunquist and Sunquist 2002) and the many different methods used to estimate population densities (Quigley and Hornocker 2010), we use pumas as a model to discuss common biases in density estimates determined using overlapping ranges of marked animals and tested them for residency and extrapolation biases. Pumas exhibit many of the traits that make density estimation problematic: sparse populations, uniform pelages making individuals difficult to identify in photographs, and large home ranges with varying degrees of overlap among individuals and between sexes (Caso et al. 2008, Logan and Sweanor 2010). Puma populations also include 'transients', sub-adult dispersers traveling in search of areas suitable for establishing residency, which may be temporarily present and detected in a given area. Finally, the spatial distribution of pumas, particularly females, is sensitive to aggregations of prey (Logan and Sweanor 2010).

Pumas have been studied intensively in a variety of habitats in North America providing an abundance of estimates of population densities (Quigley and Hornocker 2010). In contrast, only two telemetry studies have been reported from Patagonia, a vast 1 000 000 km^2, sparsely-populated region below latitude 39°S that straddles southern Chile and Argentina. Results from these two studies provided three radically different density estimates for pumas in Patagonia. Franklin et al. (1999) reported six pumas per 100 km^2 and 30 pumas per 100 km^2 for Torres del Paine National Park in southern Chilean Patagonia, and Elbroch and Wittmer (2012a) reported 3.4 pumas per 100 km^2 in the future Patagonia National Park in central Chilean Patagonia (we refer to these as the 'F6', 'F30' and 'EW' estimates, respectively). In particular, the F6 and F30 estimates are large compared to estimates reported for North America (Quigley and Hornocker 2010, Table 1).

In this paper, we explore the potential impact of residency and extrapolation bias on puma density estimates in Patagonia. We hypothesized that the F6 and F30 estimates were inflated due to residency and extrapolation biases, and that the EW estimate suffered extrapolation bias when scaled to 100 km^2. Further, we hypothesized that when these

Table 1. Unit densities (no. animals per km²) for total pumas (inclusive of kittens) as calculated from studies reviewed and presented in Quigley and Hornocker 2010. Mid-range estimates represent the middle of a reported range of densities for a given site.

	Study area (km²)	Lower	Mid-range	Upper
Alberta	780	0.027	0.037	0.047
British Columbia	54	0.035	0.036	0.037
Idaho	520	0.017	0.026	0.035
New Mexico, TA site	703	0.02	0.032	0.043
New Mexico, RA site	1356	0.017	0.028	0.039
Utah	1900	0.0058	0.0099	0.014
Montana	2500	0.0083	0.0096	0.0108
Wyoming	741	0.035	0.041	0.046
Yellowstone NP	1500	0.012	0.019	0.026
Southern Yellowstone Ecosystem	600	0.023	0.025	0.026

particular biases are accounted for, the puma density estimates reported for Torres del Paine National Park (Franklin et al. 1999), may have been approximately equivalent to the density estimates reported for the future Patagonia National Park, an ecologically similar system, in Elbroch and Wittmer (2012a); and moreover, that puma densities in southern temperate latitudes are within the range of those measured in North America (Quigley and Hornocker 2010; Table 1). We also predicted that the enumeration method of Franklin et al. (1999), when applied to the Elbroch and Wittmer (2012a) data, would result in similarly high estimates. For all estimates, we predicted linear extrapolation to larger spatial extents to introduce positive bias and extrapolation to smaller areas to introduce negative bias relative to the expected density estimates for a given sample area.

Material and methods

Franklin et al. (1999) conducted their research in the eastern portions of Torres del Paine National Park (51°05'53''W, 72°99'50''S) in southernmost Chile, and Elbroch and Wittmer (2012a) conducted their research approximately 450 km north in the southern portion of Chile's Aysén District, north of Lago Cochrane in central Chilean Patagonia (47°80'00''W, 72°00'00''S). Landscapes in both study areas were ecologically similar (Corporación Nacional Forestal 1999), and predominantly open grasslands at lower elevations interspersed with shrub communities dominated by ñirre *Nothofagus antarctica* and calafate *Berberis microphylla*. Higher elevations in both study areas included deciduous forests dominated by lenga *Nothofagus pumilio*, and both study areas included the full suite of medium and large mammals indigenous to Patagonia, including guanacos *Lama guanicoe*, huemul deer *Hippocamelus bisulcus* and culpeo foxes *Lycalopex culpaeus*, as well as exotic domestic sheep *Ovis aries* on private ranches.

The F6 density estimate was inferred from data on five individuals marked with VHF transmitters and visual sightings and track data on one additional adult male, one adult female and five kittens recorded during the winter of 1988. Locations of these animals occurred within a 200 km² study area, and the resulting density (12 pumas per 200 km²) was extrapolated downward to a unit density at 100 km² (six pumas per 100 km²). The F30 density estimate was based on an enumeration of nine unique pumas observed on a single day and reports of three additional individuals in a 40 km² portion of the 200 km² study area described above, called 'the Peninsula'; the authors used individual visual characteristics to differentiate between pumas, however, they did not differentiate between resident and transient pumas. The Peninsula is not a true peninsula, but a narrow bridge of land between Lago Sarmiento and Lago Nordenskjold (Ortega and Franklin 1995). The density estimate (12 pumas per 40 km²) was then extrapolated upward linearly to 100 km² (30 pumas per 100 km²).

The EW density estimate was calculated using proportional accounting of overlapping home ranges of resident pumas (McLellan 1989, Cooley et al. 2009) for a 450 km² area, and then extrapolated down to pumas per 100 km². First, Elbroch and Wittmer (2012a) determined the boundaries of their sampling area for estimating density, defined as the smaller area within the 1200 km² study area in which they believed they had collared all resident pumas. Then, following Cooley et al. (2009), they combined the location data for four resident females that remained completely within their smaller sampling area to form a 450 km² polygon representative of these four resident adult females. Last, Elbroch and Wittmer (2012a) summed the proportion of each additional overlapping pumas' MCPs (meaning additional female pumas that had ranges that extended beyond the 450 km² polygon and all male pumas, determined with Hawth's Tools and ArcGIS 9.1) with the 450 km² resident female polygon to determine a number of resident adult pumas for the 450 km² area; each overlapping puma was counted as the proportion of their range that overlapped with the 450 km² polygon. Adding in known kittens of marked females, they estimated the total puma density at 15.5 per 450 km² or 3.4 pumas per 100 km²). The inclusion of kittens in density estimates introduces greater variability because the number of breeding females may remain consistent over time while the number of kittens changes, however, we included kittens here for direct comparisons with Franklin et al. (1999). Elbroch and Wittmer (2012a) report densities with and without kittens for their study site.

We used the Elbroch and Wittmer (2012a) puma GPS location dataset from central Chilean Patagonia (Fig. 1) in

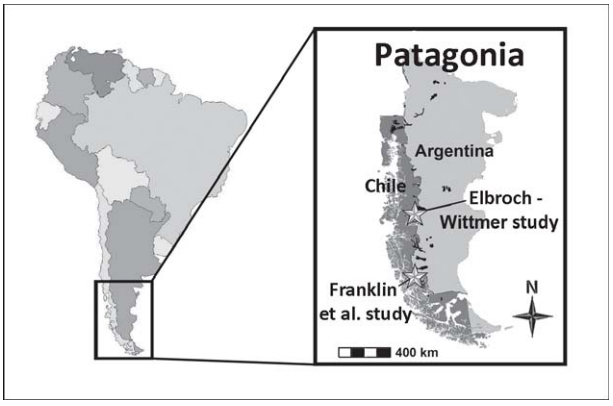

Figure 1. Locations of the Franklin et al. (1999) and Elbroch and Wittmer (2012a) study areas in Patagonia.

simulation studies to: 1) build an empirical distribution of Franklin et al. (1999) type density estimates conducted in southern Chilean Patagonia (Fig. 1); 2) measure the residency bias of their method relative to home range mapping; 3) compare the F6, F30, and EW estimates to the published record of puma estimates: and 4) measure the extrapolation bias introduced by linear extrapolation outside the original extent of all three estimates. Though the EW study site was approximately 450 km north of the Franklin et al. study site, the ecological communities, including species assemblages, were equivalent.

To assess potential residency bias in Franklin et al. (1999), we rasterized the 450 km^2 polygon for which Elbroch and Wittmer (2012a) determined their puma density, and in which they were confident they had tagged all resident pumas (Fig. 2), to a resolution of 1.5 km^2 per cell. For each raster cell, we tallied the number of adult pumas and associated kittens whose 100% MCP home ranges included that cell. We treated the cells bisected by the boundary of the aggregate 100% MCP as being completely within the study area, because the completeness of the cell has no impact on the enumeration.

We then calculated densities of total pumas (adult pumas plus kittens) as the maximum count of pumas within every possible sampling frame that fell completely within the study area. To simulate an area roughly equivalent to the Peninsula used for the F30 estimate, frames were defined using a moving window of 37.5 km^2 ('frame'; 5×5 cell square). We used 200 km^2 frames to simulate methods used to determine the F6 estimate. At this scale, we relaxed the constraint that the frames had to be fully contained by the study area, instead using the entire area of a minimum rectangle bounding the study area raster. We used five different rectangular frame dimensions (6×22, 8×16, 10×13, 12×11 and 14×10 cells) that delineated approximately 200 km^2 and sampled for maximum counts as above. These are conservative enumerations because we include no information on the portion of the frames falling outside the study area, pretending that no pumas existed anywhere but in our study areas. The different dimensions resulted in frames with area between 192 and 210 km^2, so we calculated unit densities uniquely for each frame before averaging.

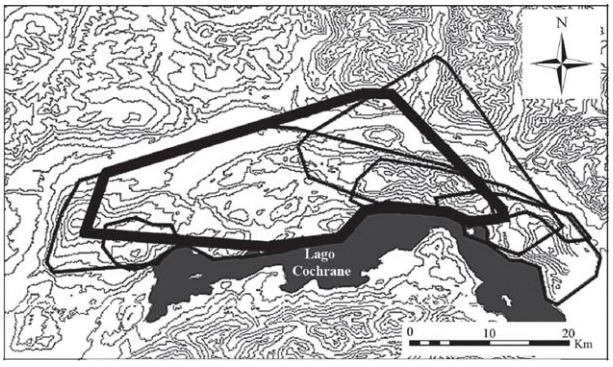

Figure 2. The study area and home ranges of pumas from Elbroch and Wittmer (2012a) used for the simulation study. The thick-lined polygon delineates the 450 km^2 polygon for which they determined their puma density, and the combined home ranges of four resident adult female pumas. The thin-lined polygons are additional puma home ranges showing partial residency within the sample area.

The resulting values simulated what we would obtain if we were able, on one day, to observe every puma having a home range intersecting that particular frame. Following Franklin et al. (1999), we treated the enumeration as the density per sampled area (37.5 km^2, 200 km^2) and extrapolated the count to 100, 200 and 450 km^2, assuming constant density (i.e. pumas $\times$ 100/37.5). We chose these reference extents because of commonality in reporting and for comparison across studies.

We measured bias in the simulated estimates ($\hat{D}_i$) relative to the EW estimate (D). Our measure of bias was the coefficient of error (CE), the root mean square deviation standardized to the magnitude of the EW estimate (D), where the root mean square error is the square root of the weighted average of the squared deviations between each enumeration-based density and that of Elbroch and Wittmer (2012a):

$$CE = \frac{\sqrt{\sum_{i=1}^{n} w_i [(\hat{D}_i - D)^2]}}{D}$$

where ($\hat{D}_i$) is the density resulting from one enumeration in the simulation (e.g. eight pumas per frame) and w_i is the frequency of that density (e.g. two frames out of 135, or 0.015). We express the CE as a percentage ($CE \times 100\%$), the percent difference from the standard of comparison.

To examine directly the bias in the linear extrapolations, we modeled the effect of study area extent on estimated unit density for puma density estimates as summarized by Quigley and Hornocker (2010). Quigley and Hornocker published ranges of values for total pumas in their review of puma density estimates. We translated the reported density estimates to unit densities based on their associated study areas. Where a range of densities was reported for a given study, we selected the middle of that range as representative and regressed the base 10 logarithm of mid-range unit densities on the base 10 logarithm of the study area (Schonewald-Cox et al. 1991, Smallwood et al. 1996, Smallwood and Smith 2001). This is a rough model of unit density that we introduced to illustrate the pattern of density estimates and their dependence on study area extent among puma density estimates reported for North America. To address the question of how well a given estimate conforms to the published record (i.e. matches the regression), we calculated two-tailed t-distribution probabilities for individual predictions for the F6, F30 and EW unit densities at their relevant study area extents.

To examine extrapolation bias, we shifted the regression line vertically to intersect the EW, F6 and F30 estimates at their original extent. Using the shifted regression, we identified the predicted unit densities for 100 km^2. This is equivalent to asking what unit densities you would expect to estimate for a 100 km^2 study, given that the published estimate is true and accurate and the regression model adequately reflects expected average unit densities. We calculated the relative bias between the reported extrapolations and the predictions as the difference between reported and predicted values, divided by the model prediction.

Table 2. Total pumas enumerated within all possible 37.5 km² frames and linear extrapolations to larger extents. The bottom row includes weighted average densities for each column.

No. of samples	Total no. of pumas	Frequency of this enumeration	Unit density	100 km²	200 km²	450 km²
2	8	0.015	0.213	21.3	42.7	95.9
9	9	0.067	0.240	24.0	48.0	108.0
41	11	0.304	0.293	29.3	58.7	131.9
15	12	0.111	0.320	32.0	64.0	144.0
14	14	0.104	0.373	37.3	74.7	167.9
54	15	0.400	0.400	40.0	80.0	180.0
Weighted averages			0.343	34.3	68.5	154.1

Results

Residency bias

Our simulation of the Franklin et al. (1999) method on the Elbroch and Wittmer (2012a) data utilized 135 different 37.5 km² sampling frames, and yielded enumerations of 8–15 pumas within the 37.5 km² sampling frames (Table 2). The distribution of the enumerations per sampling frame was skewed strongly toward the upper limit. Half of all samples obtained enumerations of 14 and 15 and only 1% had a value of 8. The resulting unit densities range from 0.21 to 0.40 pumas per km² (Table 2). The weighted average unit density for pumas was 0.343 pumas km^{-2}. The original EW estimate for these data was 0.0344 pumas km^{-2} (15.5 pumas on 450 km²). The CE for pumas was 910%, roughly an order of magnitude larger than the EW estimate.

At the 200 km² scale, 532 frames were sampled. Eighty three percent had maximum enumerations of 15 and 11% obtained 14 pumas (Table 3). In other words, 94% of the frames had maximum counts greater than 12 (no frames resulted in counts of 13). The unit densities resulting from the 200 km² frames ranged from 0.044 to 0.077 with average unit density, weighted by frequency, of 0.075; roughly twice the EW estimate (Table 3). The CE of the unit densities relative to the EW estimate was 119%.

Extrapolation bias

The log-log regression of mid-range unit density (intercept = –0.753 (0.391), slope = –0.303 (0.134), $R^2 = 0.39$) matched the EW estimate more closely than those of F6 or F30 (Fig. 3), as indicated by the following: the probability of a single unit density estimate being more extreme than EW was 0.34 ($t = 0.432$, $DF = 8$) and the same probability for F6 was less than half as great ($p = 0.15$, $t = 1.09$, $DF = 8$). The probability for F30 was 0.016 ($t = 2.61$, $DF = 8$). The points fall on the 66%, 85% and 98% confidence limits, respectively. By shifting the mid-range regression to intersect the EW estimate, the observed unit density of 0.034 on a 450 km² study area should project to a density of 5.4 pumas per 100 km² (95% confidence bounds: 2.7, 11) according to the peregression. The extrapolation of the F6 estimate is 7.4 pumas per 100 km² (3.7, 15) and that of the F30 estimate is 23 pumas/100 km² (11, 46). The relative bias at 100 km² was negative 36% for Elbroch and Wittmer (2012a), negative 19% for the F6 estimate and positive 32% for the F30 estimate. Although not reported here, we ran parallel regression and projection analyses using the lower and upper density estimates (Table 3), which produced similar results. Estimates projected 'backwards' from larger areas resulted in negative bias and the extrapolation 'forwards' from a small area to a larger one resulted in positive bias.

Discussion

Our results highlight the potential for significant bias associated with estimates of population density based on home range overlap, particularly from residency bias. Our results also supported previous suggestions to carefully consider species-specific life history and behavioral traits, and methodological limitations when estimating local densities of wide-ranging species such as pumas. More specifically, our modeling results suggest the high puma densities reported for Torres del Paine National Park in Chilean Patagonia (Franklin et al. 1999), may have been inflated due to the methods used to estimate puma density, the attributes of the study area, and particular traits of the study species.

Franklin et al. (1999) reported "minimum density estimates" (p. 35, 36) but in fact may have reported maximal estimates, because of the implicit understatement of residency area. In practical terms, a minimum density estimate would consist of the least number of animals known to occur in the

Table 3. Total pumas enumerated within 200 km² frames and linear extrapolations to smaller and larger extents. The densities at 200 km² are slightly different from the enumerations due to the use of frames that varied in area between 192 and 210 km², depending on rectangular dimensions.

No. of samples	Total no. of pumas	Frequency of enumeration	Unit density	100 km²	200 km²	450 km²
5	9	0.009	0.044	4.4	8.9	20.0
9	11	0.017	0.054	5.4	10.9	24.5
15	12	0.028	0.061	6.1	12.1	27.3
59	14	0.11	0.071	7.1	14.3	32.1
444	15	0.84	0.077	7.7	15.3	34.5
Weighted averages			0.075	7.5	15.0	33.7

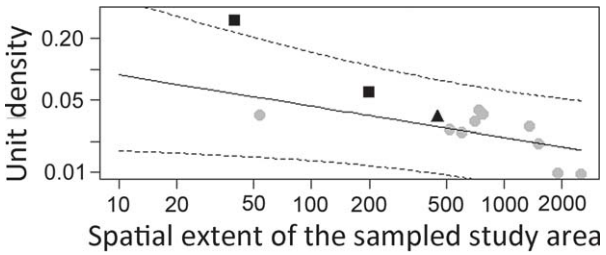

Figure 3. The mid-range regression line, on log-log scale, for total puma densities (Quigley and Hornocker 2010) with 95% prediction intervals. The Franklin et al. (squares) and Elbroch-Wittmer (triangle) estimates and regression data points (circles) are plotted for reference. All densities are 'unit densities' (no. of animals per km^2), and the values on the *y*-axis were compressed to shrink the figure.

area and attribution of their residency to minimal portions of the study area to account for the animals ranging beyond its boundaries. McLellan (1989) noted that unadjusted counts of animals whose home ranges were not circumscribed by the study area "would lead to an inflated density estimate" (p. 1857), and that "if all [animals] trapped or seen in a study area are included in the density estimate…the 'minimum' estimate may actually be higher than the true density" (p. 1857). Our simulated estimates of unit density for the Elbroch and Wittmer (2012a) data using the enumeration methods presented in Franklin et al. (1999) suggested that estimates for Torres del Paine National Park were likely positively biased due to violations with respect to residency assumptions. For example, the authors may have unintentionally introduced residency bias by including transient animals in their density estimates (we cannot know whether unmarked pumas were transient or resident), as well as an incorrect assignment of residency for pumas that were indeed residents in the area, a fact supported by the home range estimates presented by the authors. In particular, of the eight home ranges estimated for pumas in Torres del Paine National Park, only two were less than 40 km^2 or approximately equal to the area for which the F30 estimate was calculated (Franklin et al. 1999). This suggests that the Peninsula likely comprised only a portion of the home range of any puma seen there. In our simulations, we achieved roughly equivalent counts for small and large sampling frames – as expected when the method is a simple enumeration of animals visiting a sampling frame. Our results thus suggested that relating enumerated pumas to arbitrary 'sample' areas and linear extrapolation of density to new spatial extents will introduces bias, with the former being much more substantial than the latter.

Patchy distribution of resources may have further contributed to unintentionally inflated density estimates for Torres del Paine National Park. The Peninsula supported the greatest large prey density in the area (Franklin et al. 1999, p. 35) and was restricted by sharp lakeshore boundaries; as such, the Peninsula was an example of a non-representative, high quality site where many puma home ranges were likely to overlap. The highest guanaco density for the Franklin et al. study area was 15.4 guanacos km^{-2} (Ortega and Franklin 1995), but in fact considerably lower than habitat specific winter guanaco densities of 34.4 guanacos km^{-2} in mountain steppe and 71.3 guanacos km^{-2} in valley steppe habitats reported for the future Patagonia National Park in the Elbroch and Wittmer study area (Elbroch and Wittmer 2012a); even though prey densities in the respective study areas were calculated using different methods, we concluded that prey densities unlikely explained the high puma densities reported by Franklin et al. Nevertheless, given the small size of the Franklin et al. study area, it may be possible that wide-ranging pumas were subsidized by the thousands of domestic sheep immediately adjacent Torres del Paine (Ortega and Franklin 1995).

Had Elbroch and Wittmer (2012a) randomly chosen one of our sampling frames and seen all pumas therein, they would have had a 92% chance of counting 11 or more pumas and a 50% chance of counting more than 12 pumas. Therefore, our modeling results suggest that the true density of the Franklin et al. (1999) study site in southern Chilean Patagonia population may have been approximately equivalent to or potentially less than that calculated by Elbroch and Wittmer (2012a).

Because the Franklin et al. puma density estimates have been the sole estimates for this species in Patagonia for many years, there is also the possibility that their densities have been used to justify or design current puma management strategies for the region. Currently, bounties for killing pumas are provided in the three large Argentine Patagonia provinces of Río Negro, Chubut, and Santa Cruz (which account for 72% of all of Patagonia). Pumas are currently subject to sport-hunting regulations in the remaining Argentine Patagonia provinces of Neuquén and La Pampa, and can be legally killed in Chilean Patagonia with a depredation permit (Walker and Novaro 2010). Our modeling results suggest that a review of puma densities and subsequent management may be warranted in Patagonia.

Overexploitation of puma populations can occur quickly, even as indices of density, such as complaints of puma–human conflicts, increase (Lambert et al 2006). As the largest predator in southern South America, pumas have the potential to be both a flagship species for identifying and protecting wildlife corridors and an umbrella species in large-scale conservation efforts in future conservation strategies in South America (Elbroch et al. 2009, Kissling et al. 2009, Walker and Novaro 2010). Pumas also provide keystone roles in Patagonia, supporting biodiversity inclusive of near-threatened Andean condors (*Vultur gryphus*; BirdLife International 2008, Elbroch and Wittmer 2012b), found across Patagonia.

Non-invasive survey methods, including remote camera surveys (Long et al. 2008) and DNA based scat surveys (Long et al. 2008, Brinkman et al. 2011), have provided promising alternatives to the home range overlap method of determining animal density. Nevertheless, camera surveys are still largely limited to providing relative estimates of population densities for carnivores with distinct individual characteristics such as spots or stripes (Karanth and Nichols 1998, Silver et al. 2004, Dillon and Kelly 2008); the identification of individuals is a prerequisite to mark–recapture techniques (Foster and Harmsen 2012). Capture–recapture methods based on genetic material recovered in scats are also improving, but non-trivial obstacles to reliable density estimates persist in the form of genotyping errors, improper study design, and the logistics of obtaining rigorous samples (Marucco et al. 2011), all of which can introduce substantial

bias to density estimates. For wide-ranging, low-density species that cannot be individually identified visually, radio-telemetry and spatially-explicit (genetic) capture–recapture (SECR; Gardner et al. 2010, Noss et al. 2012) are the only viable options for density estimation. SECR does not require ad hoc estimates of mean maximum distance moved (MMDM) used in capture–recapture studies to determine species density (Wilson and Anderson 1985, Karanth and Nichols 1998), but it does require other limiting assumptions and sampling requirements that may not be appropriate to terrestrial carnivores (Foster and Harmsen 2012); thus, radio-telemetry remains the most viable option for certain carnivore species, pumas among them.

Acknowledgements – Funding for the Elbroch and Wittmer fieldwork was provided by the National Science Foundation, National Geographic Society, Felidae Conservation Fund, Conservación Patagonica, Oregon Zoo Future for Wildlife Program, and the American Society of Mammalogists. Funding for this analysis was drawn from a National Science Foundation Graduate Fellowship and the Robert and Patricia Switzer Foundation.

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