# Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity?<sup>1</sup>

Erlend B. NILSEN, Department of Forestry and Wildlife Management, Hedmark University College, N-2480 Koppang, Norway and Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, N-0316, Oslo, Norway.

Ivar HERFINDAL, Department of Biology, Norwegian University of Science and Technology,

N-7491 Trondheim, Norway.

John D. C. LINNELL<sup>2</sup>, Norwegian Institute for Nature Research, Tungesletta 2,

N-7485 Trondheim, Norway, e-mail: john.linnell@nina.no

*Abstract:* Carnivore home-range sizes vary profoundly between populations within a species. One commonly cited reason for this is variation in prey population density and environmental productivity. However, obtaining reliable measures of prey density in the field is both time and effort consuming. Therefore, a methodology that enabled scientists and managers to extrapolate home-range sizes across areas would be a valuable tool. So far, the potentials of different remote-sensing indices to represent environmental productivity have been poorly evaluated in this context. In this study, we have evaluated the utility of a readily available remote-sensing index, the Fraction of Photosynthetically Active Radiation absorbed by vegetation canopies (FPAR), to explain interpopulation variation in home-range size for 12 carnivore species. In multiple regression models, evaluated by the Bayesian Information Criterion (BIC), we found that the FPAR index added predictive power to the models for eight of the species. The explanatory power varied between 16% and 71% for the different species. We suggest that using remote-sensing indices such as FPAR to predict area specific home-range sizes for carnivores explanatory power for some species.

Keywords: carnivores, FPAR, home-range size, intra-specific variation, remote sensing.

*Résumé* : La dimension du domaine vital des carnivores varie énormément entre les populations d'une même espèce. Une des raisons souvent mentionnées pour expliquer ce phénomène est la variation de la densité de population des proies et de la productivité environnementale. L'obtention de données fiables sur la densité des proies demande beaucoup de temps et d'effort. Par conséquent, une méthode permettant aux scientifiques et aux gestionnaires d'extrapoler les dimensions des domaines vitaux peu importe où l'on se trouve serait un outil précieux. Or, le potentiel des différents indices de télédétection donnant des renseignements sur la productivité environnementale n'a pas encore été évalué à sa juste valeur. Dans cette étude, nous avons vérifié l'utilité d'un indice de télédétection déjà disponible, la fraction de radiation photosynthétiquement active (FRPA) qui est absorbée par les couverts de végétation, pour expliquer la variation de la taille du domaine vital entre les populations de douze espèces de carnivores. Dans les modèles de régression multiple, nous avons trouvé que l'indice de la FRPA ajoute un pouvoir prédictif aux modèles pour huit des douze espèces à l'étude. Le pouvoir explicatif varie de 16 à 71% selon les espèces. Nous suggérons que l'utilisation d'indices de télédétection, comme la FRPA, pourrait être un outil puissant pour prédire les dimensions de domaines vitaux des carnivores. Il est toutefois nécessaire de continuer à développer cette méthodologie de façon à la rendre plus performante. *Mots-clés* : carnivores, FRPA, taille du domaine vital, télédétection, variation intraspécifique.

Nomenclature: MacDonald, 2001.

#### Introduction

After centuries of persecution and eradication campaigns, most countries are aiming to conserve their carnivores (Mech, 1996; Treves & Karanth, 2003). However, despite this notable change in attitude, there are still a lot of challenges associated with the preservation and management of carnivores. These challenges include conflicts associated with depredation on domesticated livestock (Odden *et al.*, 2002), competition for game animals (Mech & Nelson, 2000), fear and social conflict (Conforti & de Azevedo, 2003; Ericsson & Heberlein, 2003), and direct and indirect threats to human life (Kruuk, 2002). But other factors associated with the ecology of carnivores also pose a challenge to their conservation. For example, they usually use very large individual home ranges (Linnell *et al.*, 2001), indicating that carnivores usually need to be preserved within vast areas of land. A consequence of this is that reserve size is highly correlated with risk of extinction in carnivores and that a species' home-range size is a good predictor of its extinction probability within protected areas (Woodroffe & Ginsberg, 1998; Woodroffe, 2000).

Home-range size and shape is one of the most fundamental ecological parameters for a species and is indeed one of the most thoroughly studied aspects of species

<sup>&</sup>lt;sup>1</sup>Rec. 2004-04-21; acc. 2004-09-23.

Associate Editor: André Desrochers.

<sup>&</sup>lt;sup>2</sup>Author for correspondence.

ecology (field surveys: e.g., Landa et al., 1998; Linnell et al., 2001; comparative approach: e.g., Harestad & Bunnell, 1979; Gittleman & Harvey, 1982; Kelt & Van Vuren, 2001; Grigione et al., 2002). Besides being studied for its own sake, knowing the spatial scale at which natural processes operate is fundamental to making informed decisions in wildlife management and conservation (Sutherland, 1998; Smallwood, 2001). A typical practical imperative is to define a minimum area suitable to contain the movements of individuals or a viable population. For the latter, reliable measures of minimum viable population size are needed together with knowledge about the space requirements of individuals. Furthermore, home-range sizes are often used when producing population estimates, either through the application of formal distance rules or when extrapolating from species distribution to population size (Rabinowitz, 1993; Gros, Kelly & Caro, 1996). Consequently, home-range sizes of carnivores are important in many aspects of their conservation and management.

Unfortunately, home-range sizes vary between carnivore species by at least several orders of magnitude. Much of this variation is clearly due to differences in body size, feeding habits, and habitat (Harestad & Bunnell, 1979; Kelt & Van Vuren, 2001). However, even within a species there can be differences in home-range size by two orders of magnitude (McLoughlin, Ferguson & Messier, 2000; E. B. Nilsen & J. D. C. Linnell, unpubl. data). This variation at both the inter- and intraspecific levels makes it very difficult to transfer results from one study area to another, and, clearly, extrapolating data that can have a potential error of an order of magnitude or more is unacceptable. There is therefore a need to obtain better site-specific estimates of home-range size. However, measuring carnivore home ranges is logistically demanding, as it involves both capturing and frequent radio-tracking of a large sample of individuals to get a reliable measure of their space use patterns. In addition, when species are highly endangered there may be a reluctance to utilize invasive methods such as telemetry.

Home-range size variation is also often reported to be due to prey population density (Carbone & Gittleman, 2002). However, estimating prey density can also be prohibitively expensive and logistically difficult. Early studies have revealed, however, that herbivore biomass often correlates with patterns of productivity (East, 1984). Fortunately, recent advances in remote-sensing technology have made different productivity indices readily available. The different remote-sensing indices are rough indicators of green biomass, which is known to reflect prey density reasonably well (McNaughton *et al.*, 1989). So far, the indices have been successful in explaining patterns in both biodiversity distribution (Bawa *et al.*, 2002) and Eurasian lynx (*Lynx lynx*) space use (Herfindal *et al.*, 2005).

The aim of this study is to evaluate the ability of a readily available remote sensing index, the Fraction of Photosynthetically Active Radiation (FPAR) to explain variation in home-range size within a species for some selected species of carnivores for which data from a wide range of study areas is available. More specifically, we predict that home-range size should decrease with increasing environmental productivity (Harestad & Bunnell, 1979; Carbone & Gittleman, 2002). Furthermore, we investigate whether the home-range sizes were affected by environmental seasonality, as shown by McLoughlin, Ferguson, and Messier (2000) for grizzly bear (*Ursus arctos*) and Herfindal *et al.* (2005) for Eurasian lynx.

## Methods

#### DATA COLLECTION

We collected data on home-range size from the literature for 12 species of carnivores. In addition, we obtained original data from unpublished studies on request. When combining both published and unpublished studies, a total of 199 studies were included in the analyses. Most study areas were located in the Northern Hemisphere, except for leopard (*Panthera pardus*) studies. An overview of which species are included, the number of studies for each species, and mean estimates of home-range size is given in Table I. A complete list of studies included in the analyses is available from the authors on request. For the solitary species, we obtained sex-specific means for each study site, whereas we used group range size for group-living species. We included only resident adults in our analyses, and only annual or composite home ranges

TABLE I. Mean sex-specific home-range (HR) size and number of studies for each species. In the table, mean home-range size (SD in parentheses) is given.

Common name	Latin name	Males		Females	
		Number of studies	Mean HR size in km <sup>2</sup>	Number of studies	Mean HR size in km <sup>2</sup>
Brown bear	Ursus arctos	30	1,060 (1,506)	32	351 (472)
Black bear	Ursus americanus	18	232 (399)	21	34 (34)
Wolverine	Gulo gulo	7	621 (438)	7	259 (122)
American marten	Martes americana	8	12 (14)	8	8 (9)
Fisher	Martes pennanti	7	25 (14)	7	10 (5)
Leopard	Panthera pardus	11	179 (327)	9	71 (100)
Canadian lynx	Lynx canadensis	13	153 (112)	11	85 (58)
Bobcat	Lynx rufus	24	43 (29)	23	20 (13)
Puma	Puma concolor	17	352 (218)	20	193 (177)
GROUP OR PACK HR					
Wolf	Canis lupus	25	611 (511)		
Coyote	Canis latrans	18	42 (34)		
Red fox	Vulpes vulpes	11	10 (8)		

are included, to prevent biases caused by seasonal differences in home-range size (Linnell *et al.*, 2001; Grigione *et al.*, 2002). All home-ranges are based on radio-tracking and estimated by either 100% or 95% minimum convex polygon (MCP). We included only species for which we were able to obtain at least seven studies. We did not include urban populations, as remotely sensed productivity indices are not likely to provide valid indices of prey availability in such areas.

For red foxes (*Vulpes vulpes*) and coyotes (*Canis latrans*), various authors reported either sex-specific home ranges or group home ranges. We treated all the studies for these species as though they were for group home ranges. Thus, when an author reported sex-specific home ranges, we used the sex with the largest home-range, as this value best represents the home range for the pack or family group.

#### THE FPAR INDEX

The Fraction of Photosynthetically Active Radiation (0.4-0.7 µm) absorbed by vegetation (FPAR) characterizes vegetation canopy functioning and absorption capacity (Myneni et al., 2002). We used this index as a measure of habitat productivity. We downloaded monthly MODIS FPAR images (4-  $\times$  4-km cells) from the NASA MODIS home page (http://modis-land.gsfc.nasa.gov) for the period October 2000 through October 2002. When a value existed for a given cell from both years, we used the mean value for that month. If the value was missing one year, due to clouds, other atmospheric conditions, or polar night, we used the value from the single year. This problem was mostly evident in northern areas. Using the monthly values, we produced two new maps: one representing mean annual FPAR as an index of overall productivity and the other using the standard deviation of the 12 monthly values for each cell as an index of environmental seasonality. The images were processed using ERDAS Imagine software (ERDAS inc., Atlanta, Georgia, USA).

For each study site, we drew a circle with an area corresponding to the size of the study area. The size of the study was either given by the authors of the specific study or calculated by multiplying the mean home-range size for that study by the number of home ranges. If the number of home ranges was not given by the author, we multiplied the mean home-range size by 10. As not all geographical co-ordinates were given accurately enough to be placed within one  $4- \times 4$ -km cell for all study sites, we set the minimum study area to 50 km<sup>2</sup>, representing *ca* four cells. Within this circle, we calculated the mean value of the pixels from both images, one representing mean annual FPAR for the study site and the other representing annual standard deviation in FPAR.

#### STATISTICAL ANALYSES

We used mean annual FPAR as a measure of habitat productivity and annual standard deviation in FPAR as a measure of seasonality. However, these two variables were not independent. We therefore fitted species-specific linear regressions between these two variables, using standard deviations in FPAR as the dependent variable. We used the standardized residuals from this regression as a measure of seasonality. Prior to the analyses, we  $\log_{10}\text{-transformed}$  the home-range areas (ha) in order to stabilize the variance (Sokal & Rohlf, 1995). The log<sub>10</sub>-transformed mean sex-specific home-range area was used as the dependent variable in the model for solitary species, with sex as a covariate. In the global model, we included the full interaction between productivity, seasonality, and sex for the solitary species. For the group-living species, the global model included the full interaction between productivity and seasonality. The most parsimonious models were selected using the Bayesian information criterion (BIC), also known as Schwarz's Bayesian criterion (Burnham & Anderson, 2002). Bayesian information criterion is a more conservative criterion than Akaike information criterion (AIC) (Miller, 2002; Kadane & Lazar, 2004) and differs from AIC with respect to how the numbers of parameters are weighed compared with the sample size (Burnham & Anderson, 2002; Kadane & Lazar, 2004). Bayesian information criterion is obtained as  $-2 \times \text{log-likelihood} + n_{\text{par}} \times \log(n_{\text{obs}})$ , where  $n_{par}$  represents the number of parameters and  $n_{obs}$  the number of observations in the fitted model. When the difference in BIC (termed  $\triangle$ BIC) was < 2, we regarded the models as equally plausible (Burnham & Anderson, 2002). We fitted individual models for each species. All statistics were run in S-plus version 2000 (Insightful Corporation, Seattle, Washington, USA).

## Results

There is a profound intra-specific variation in homerange size between the different study areas, as shown by high SD values (Table I). This result further demonstrates the importance of being able to predict area-specific home ranges.

The results from the model-fitting are shown in Table II. For the brown bear and leopard, the models with lowest BIC values included a main effect of productivity (Figure 1). For wolverine (Gulo gulo), Canadian lynx (Lynx canadensis), bobcat (Lynx rufus), and coyote (Canis latrans) the selected models, based on BIC, included a main effect of season (Figure 2). In addition, the interaction between productivity and seasonality was included in the selected model for fisher (Martes pennanti) and grey wolf (Canis lupus) (Figure 3). Consequently, for eight of 12 species, productivity, seasonality, or the interaction term was included in the best model (*i.e.*, the model with the lowest BIC value) and thus added significant predictive power to the models. For the four remaining species, red fox, American marten (Martes americana), black bear (Ursus americanus), and puma (Puma concolor), our remote-sensing index was not included in the selected models.

Investigation of the parameter estimates (Table III) for the best models for the species where the main effect of productivity was included determined that the relationship was negative for all species. This implies that home-range size decreased as productivity increased. However, the relationship was significant at  $\alpha = 0.05$  only for the grey wolf, leopard, and brown bear. The relationship between seasonality and home range is, however, somewhat more complex, as the relationship is negative for Canadian lynx, wolverine, and fisher, but is positive for the grey wolf, coyote (borderline significant term), and bobcat.

TABLE II. Summary of the results from the model selection, based on Bayesian information criterion (BIC). Only models with a  $\Delta$ BIC of less than two compared with the best model are listed, as these models are generally regarded as equally parsimonious. For the solitary species, the global model included the full interaction between sex, productivity (prod), and seasonality (seas). For the group-living species, the global model included the interaction between productivity and seasonality. The smallest model included only the intercept. All possible models were run.

	BIC	ΔBIC	<i>R</i> <sup>2</sup>
$\overline{Ursus\ arctos\ (n=62)}$			
sex + prod	96.17	-	0.32
Ursus americanus $(n = 39)$			
sex	65.10	-	0.31
Gulo gulo $(n = 14)$			
sex + seas	9.45	-	0.44
sex	9.51	0.06	0.32
sex + prod + seas	11.26	1.81	0.47
Martes americana $(n = 16)$			
intercept only	26.70	-	
seas	27.43	0.73	0.12
Martes pennanti $(n = 14)$			
sex + prod + seas + prod:seas sex + seas + prod	4.39	-	0.71
+ sex:seas + prod:seas	5.11	0.72	0.75
Panthera pardus $(n = 20)$			
sex + prod	27.00	-	0.59
sex + prod + seas	28.42	1.42	0.62
prod	28.84	1.84	0.47
$I_{NNX}$ canadensis $(n = 24)$			
sex + seas	21.59	-	0.26
seas	21.76	0.17	0.14
intercept only	22.32	0.73	
Lynx rufus $(n = 47)$			
sex + seas	50.56	-	0.35
Puma concolor $(n = 37)$			
sex	29.89	-	0.21
sex + seas	30.94	1.05	0.26
sex + prod	31.77	1.88	0.25
Canis lupus $(n = 25)$			
prod + seas + prod:seas	24.79	-	0.59
Canis latrans $(n = 18)$			
seas	32.63	-	0.16
intercept only	32.96	0.33	
Vulpes vulpes $(n = 11)$			
intercept only	19.85	-	
prod	20.68	0.83	0.13

A striking, but not surprising, feature of the results for the solitary species is that males generally have larger home-ranges than females (except for American marten). This is an almost universal finding (e.g., Landa et al., 1998; McLoughlin & Ferguson, 2000; Linnell et al., 2001; see Sandell, 1989 for a discussion), probably caused by differences both in body mass and in reproductive strategies. There was, however, no interaction between sex and either of the variables (productivity and seasonality) in any species. This implies that both sexes respond equally to environmental factors. However, since we log<sub>10</sub>-transformed the home-range area prior to the analyses, the relationship is multiplicative rather than additive. This means that the relative difference in homerange size between the sexes is the same, but the absolute difference (in km<sup>2</sup>) becomes larger as the mean area specific size increases.

# Discussion

McLoughlin and Ferguson (2000) suggested that food availability and habitat productivity are the primary determinants of variation in home-range size between populations. In this study we have evaluated the practical usage of a readily available remote-sensing index representing primary production and seasonality to predict carnivore home-range sizes at the population scale. Our results suggest that using remote-sensing indices to predict homerange sizes for carnivores could provide valuable information, but also that species-specific factors need to be considered. Consequently, the predictive power varied between the species. For species such as leopard, wolf, and fisher, the selected models including seasonality and/or productivity explained much (59%, 59%, and 71%, respectively) of the variation in home-range sizes. However, for other species, such as American marten, black bear, red fox, and puma, the FPAR index did not add predictive power to the models.

To our knowledge, no previous studies have used remote-sensing indices to predict carnivore home-range size at the population level (except Herfindal et al., 2005 for Eurasian lynx), although McLoughlin et al. (2003) used remote sensing to categorize habitat types for grizzly bears and found that individuals inhabiting areas with marginal habitats utilized larger home ranges. Some attempts have been made to compare home-range sizes at the population scale across latitudinal gradients (Gompper & Gittleman, 1991). Unfortunately, latitude can be a very poor indicator of productivity, as it does not consider the possible modulating effects of ocean currents, altitude, and rainfall. Other attempts to investigate the relationship between carnivore space use and prey densities have usually been based on field surveys of prey densities (Carbone & Gittleman, 2002), which are demanding in time and effort. In contrast, FPAR is an index that reflects the fraction of incident photosynthetically active radiation absorbed by the green leaves in the canopy, which could be used as a measure of net primary production (Sellers et al., 1997). This type of data has not yet been used very much in explaining ecological patterns (but see Bawa et al., 2002 and Herfindal et al., 2005, for examples), although FPAR seems to be a good measure of the primary productivity of an area, which is known to influence the entire food web (McNaughton et al., 1989).

The multiple regressions, with model selection based on BIC, enabled us to test the relative importance of the factors. Examining the parameter estimates (Table III), it is obvious that the relationship between home-range area and mean FPAR is as predicted for all the species: larger home range areas with decreasing productivity. Thus, the lack of relationship for some species might be caused by low sample size. However, there are also other possible explanations for the lack of predictive power of the FPAR index for some of the species, including both biological and methodological factors. One potential methodological explanation is related to the fragmentation of the landscape matrix. At the one-cell scale (*i.e.*,  $4 \times 4$  km), the cell represents the mean value within its borders. However, in fragmented landscapes, each cell might con-



FIGURE 1. The relationship between home-range size and productivity for brown bear (a) and leopard (b). Observed values for females (filled circles) and males (open circles) and the predicted relationship from the selected model for females (dashed line) and males (solid line) appear in the same figure. Note that the home-range size is back-transformed from  $\log_{10}$  scale to linear scale. Productivity was estimated as the fraction of photosynthetically active radiation absorbed by the vegetation.

tain a range of habitat types. Often, a species will not equally utilize all habitat types within a given landscape matrix. Thus, there might be a mismatch between the measured cell value and the actual value (as experienced by an individual animal) for that cell when taking habitat use into account. This problem is also evident at the study-area scale, as all cells within the study area are equally weighted in our analysis. This might be the reason for the lack of relationship in the American marten, which is highly selective of forest age classes in its habitat use (Potvin, Belanger & Lowell, 2000; Smith & Schaefer, 2002). Consequently, the FPAR index might be biased by surrounding landscape (in the case of marten this would mean forest stands of various ages) that is not used by the individuals. Carnivore space use can also be heavily influenced by the structure of the carnivore guild, with smaller species being excluded from areas by larger competitors (Linnell & Strand, 2000). Therefore, the guild structure in each study area could also influence the environment-home-range-size relationship.

One potential biological reason for the lack of relationship between our productivity index and home-range size for black bear and red fox is that these species utilize a wide range of food sources. Harestad and Bunnell (1979) have shown that strict carnivores usually utilize larger areas than omnivorous ones. These three species show a great deal of intra-specific variation in diet (E. B. Nilsen & J. D. C. Linnell, data on file), including large and small mammals, birds, fruits and other mast, and carrion. This diet variation might influence home-range size, hiding the expected relationship.

In our analysis, we found that some species increased their home-range area as seasonality increased, and other species showed a reverse pattern. The reason for this is not obvious to us, considering that, e.g., the bobcat and Canadian lynx did not show the same patterns, although they live sympatrically in at least parts of their range. One possible explanation is that Canadian lynx and fisher to some extent specialize on snowshoe hares (Lepus amer*icanus*), which tend to have a northern distribution, *i.e.*, in areas with greater seasonality and lower productivity. McLoughlin, Ferguson, and Messier (2000) reported that home-range area increased with seasonality in grizzly bears. However, they also found a non-linear relationship between home-range overlap and seasonality, indicating that the relationship between seasonality and patterns of space use is not straightforward.

Despite the fact that we did not find significant results for all species, the fact that all the relationships had a direction consistent with the predictions indicates that it is highly likely that prey density (here indexed by productivity) is one of the major determinants of intraspecific variation in home-range size, thus confirming a widely held assumption about factors influencing carnivore space use (Sandell, 1989; McLoughlin & Ferguson, 2000). This also opens the possibility of using FPAR as a conservation tool to help predict species home-range size in situations where no better species-specific predictor data is available. After extensive searching of the literature we found 12 species for which seven or more telemetry studies were available. These species are widespread, well studied, and relatively common and occur in coun-





FIGURE 2. The relationship between home-range size and seasonality for wolverine (a), Canadian lynx (b), bobcat (c), and coyote (d). Observed values for females (filled circles) and males (open circles) and the predicted relationship from the selected model for females (dashed line) and males (solid line) appear in the same figure (for the coyote, filled circles represent pack values). Note that the home-range size is back-transformed from log<sub>10</sub> scale to linear scale. See methods for details on seasonality estimates.

FIGURE 3. The relationship between home-range size, and seasonality and productivity for wolf (a) and male (b) and female (c) fisher. Note that the home-range size is back-transformed from  $\log_{10}$  scale to linear scale. See Methods for detail on productivity and seasonality estimates.

Species	Variable	Beta	SE	<i>t</i> -value	Р
Ursus arctos	Sex (female – male)	-0.530	0.120	4.42	< 0.001
	Productivity	-1.183	0.404	-2.928	0.005
Gulo gulo	Sex (female – male)	-0.366	0.141	2.605	0.025
	Seasonality	-1.641	1.074	-1.528	0.155
Martes pennanti	Sex (female – male)	-0.388	0.107	3.614	< 0.006
	Productivity	-0.511	0.711	0.719	0.490
	Seasonality	-79.926	25.733	-3.106	0.013
	Productivity : Seasonality	121.289	39.712	3.054	0.014
Puma pardus	Sex (female – male)	-0.370	0.172	2.156	0.046
	Productivity	-2.231	0.507	-4.397	< 0.001
Lynx canadensis	Sex (female – male)	-0.226	0.128	1.775	0.090
	Seasonality	-2.075	1.005	-2.064	0.052
Lynx rufus	Sex (female – male)	-0.288	0.106	2.722	0.009
	Seasonality	2.343	0.590	3.969	< 0.001
Canis lupus	Productivity	-1.099	0.368	-2.956	0.008
	Seasonality	9.456	2.339	4.043	< 0.001
	Productivity : Seasonality	-13.719	4.694	-2.923	0.008
Canis latrans	Seasonality	2.023	1.143	1.771	0.095

TABLE III. Parameter estimates for the best models for each species. Only parameter estimates for the models with the lowest Bayesian information criterion (BIC) (from Table II) are given, although two or more models may be equally parsimonious (*i.e.*,  $\Delta$ BIC < 2). Only species where seasonality, productivity, or the interaction term was included in the selected model are shown in the table.

tries that are in general able to afford telemetry studies (with the leopard as a possible exception). In such cases, it is unlikely that FPAR data will be the optimal type of data for management/conservation purposes. Furthermore, the high degree of unexplained variation revealed in our analyses indicates that further factors should be included in analyses where greater precision is required. However, the order Carnivora contains approximately 226 species, most of which have never been studied using telemetry and many of which live in remote areas. Our results from this study indicate that FPAR or similar remotely sensed data may be a useful parameter to include in models that try to predict the home-range size of under-studied species, if other factors such as body weight and diet can be included in the analyses.

## Acknowledgements

We would like to thank all those researchers who have kindly sent us their unpublished home-range estimates. Furthermore, we would like to thank the Norwegian Research Council for financial support and three anonymous referees for useful comments on an earlier draft.

#### Literature cited

- Bawa, K., J. Rose, K. N. Ganeshaiah, N. Barve, M. C. Kiran & R. Umashaanker, 2002. Assessing biodiversity from space: An example from the Western Ghats, India. Conservation Ecology, 6: 7. [online] URL: http://www.consecol.org/vol6/iss2/art7
- Burnham, K. P. & D. R. Anderson (eds.), 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. 2<sup>nd</sup> Edition. Springer, New York, New York.
- Carbone, C. & J. L. Gittleman, 2002. A common rule for the scaling of carnivore density. Science, 295: 2273-2276.
- Conforti, V. A. & F. C. C. de Azevedo, 2003. Local perceptions of jaguars (*Panthera onca*) and pumas (*Puma concolor*) in the Iguacu National Park area, south Brazil. Biological Conservation, 111: 215-221.

- East, R., 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. African Journal of Ecology, 22: 245-270.
- Ericsson, G. & T. A. Heberlein, 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. Biological Conservation, 111: 149-159.
- Gittleman, J. L. & P. H. Harvey, 1982. Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology, 10: 57-63.
- Gompper, E. & J. L. Gittleman, 1991. Home range scaling: Intraspecific and comparative trends. Oecologia, 87: 343-348.
- Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald & M. L. Johnson, 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). Animal Conservation, 5: 317-324.
- Gros, P. M., M. J. Kelly & T. M. Caro, 1996. Estimating carnivore densities for conservation purposes: Indirect methods compared to baseline demographic data. Oikos, 77: 197-206.
- Harestad, A. & F. Bunnell, 1979. Home range and body weight - A reevaluation. Ecology, 60: 389-402.
- Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen & R. Andersen, 2005. Prey density and environmental productivity explain variation in Eurasian lynx home-range size at two spatial scales. Journal of Zoology, 265: 63-71.
- Kadane, J. B. & N. A. Lazar, 2004. Methods and criteria for model selection. Journal of the American Statistical Association, 99: 279-290.
- Kelt, D. A. & D. H. Van Vuren, 2001. The ecology and macroecology of mammalian home range area. American Naturalist, 157: 637-645.
- Kruuk, H. (ed.), 2002. Hunter and Hunted, Relationships between Carnivores and People. Cambridge University Press, Cambridge.
- Landa, A., O. Strand, J. D. C. Linnell & T. Skogland, 1998. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. Canadian Journal of Zoology, 76: 448-457.
- Linnell, J. D. C. & O. Strand, 2000. Conservation implications of aggressive intra-guild interactions among mammalian carnivores. Diversity and Distributions, 6: 169-176.

- Linnell, J. D. C., R. Andersen, T. Kvam, H. Andren, O. Liberg, J. Odden & P. F. Moa, 2001. Home range size and choice of management strategy for lynx in Scandinavia. Environmental Management, 27: 869-879.
- MacDonald, D. W. (ed.), 2001. The New Encyclopedia of Mammals. Oxford University Press, Oxford.
- McLoughlin, P. D. & S. H. Ferguson, 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. Écoscience, 7: 123-130.
- McLoughlin, P. D., S. H. Ferguson & F. Messier, 2000. Intraspecific variation in home range overlap with habitat quality: A comparison among brown bear populations. Evolutionary Ecology, 14: 39-60.
- McLoughlin, P. D., H. D. Cluff, R. J. Gau, R. Mulders, R. L. Case & F. Messier, 2003. Effect of spatial differences in habitat on home ranges of grizzly bears. Ecoscience, 10: 11-16.
- McNaughton, S. J., M. Oesterheld, D. A. Frank & K. J. Williams, 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. Nature, 341: 142-144.
- Mech, L. D., 1996. A new era for carnivore conservation. Wildlife Society Bulletin, 24: 397-401.
- Mech, L. D. & M. E. Nelson, 2000. Do wolves affect whitetailed buck harvest in northeastern Minnesota? Journal of Wildlife Management, 64: 129-136.
- Miller, A. J. (ed.), 2002. Subset Selection in Regression. Chapman & Hall, London.
- Myneni, R. B., S. Hoffmann, Y. Knyazikhin, J. L. Privette, J. Glassy, Y. Tian, Y. Wang, X. Song, Y. Zhang, G. R. Smith, A. Lotsch, M. Friedl, J. T. Morisette, P. Votava, R. R. Nemani & S. W. Running, 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sensing of Environment, 83: 214-231.
- Odden, J., J. D. C. Linnell, P. F. Moa, I. Herfindal, T. Kvam & R. Andersen, 2002. Lynx depredation on domestic sheep in Norway. Journal of Wildlife Management, 66: 98-105.

- Potvin, F., L. Belanger & K. Lowell, 2000. Marten habitat selection in a clearcut boreal landscape. Conservation Biology, 14: 844-857.
- Rabinowitz, A., 1993. Estimating the Indochinese tiger Panthera tigris corbetti population in Thailand. Biological Conservation, 65: 213-217.
- Sandell, M., 1989. The mating tactics and spacing behaviour of solitary carnivores. Pages 164-182 in J. L. Gittleman (ed). Carnivore Behavior, Ecology and Evolution. Cornell University Press, Ithaca, New York.
- Sellers, P. J., R. E. Dickinson, D. A. Randall, A. K. Betts, F. G. Hall, J. A. Berry, G. J. Collatz, A. S. Denning, H. A. Mooney, C. A. Nobre, N. Sato, C. B. Field & A. Henderson-Sellers, 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. Science, 275: 502-509.
- Smallwood, K. S., 2001. Linking habitat restoration to meaningful units of animal demography. Restoration Ecology, 9: 253-261.
- Smith, A. C. & J. A. Schaefer, 2002. Home-range size and habitat selection by American marten (*Martes americana*) in Labrador. Canadian Journal of Zoology, 80: 1602-1609.
- Sokal, R. R. & F. J. Rohlf, 1995. Biometry. 3<sup>rd</sup> Edition. W. H. Freeman and Company, New York, New York.
- Sutherland, W., 1998. The importance of behavioural studies in conservation biology. Animal Behaviour, 56: 801-809.
- Treves, A. & U. Karanth, 2003. Human-carnivore conflict and perspectives on carnivore management. Conservation Biology, 17: 1491-1499.
- Woodroffe, R., 2000. Predators and people: Using human densities to interpret declines of large carnivores. Animal Conservation, 3: 165-173.
- Woodroffe, R. & J. R. Ginsberg, 1998. Edge effects and the extinction of populations inside protected areas. Science, 280: 2126-2128.