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Wolves adapt territory size, not pack size to local habitat quality

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Summary

1. Although local variation in territorial predator density is often correlated with habitat quality, the causal mechanism underlying this frequently observed association is poorly understood and could stem from facultative adjustment in either group size or territory size.

2. To test between these alternative hypotheses we used a novel statistical framework to construct a winter population-level utilization distribution for wolves (*Canis lupus*) in northern Ontario, which we then linked to a suite of environmental variables to determine factors influencing wolf space use. Next we compared habitat quality metrics emerging from this analysis as well as an independent measure of prey abundance, with pack size and territory size to investigate which hypothesis was most supported by the data.

3. We show that wolf space use patterns were concentrated near deciduous, mixed deciduous/coniferous and disturbed forest stands favoured by moose (*Alces alces*), the predominant prey species in the diet of wolves in northern Ontario, and in proximity to linear corridors, including shorelines and road networks remaining from commercial forestry activities.

4. We then demonstrate that landscape metrics of wolf habitat quality – projected wolf use, probability of moose occupancy and proportion of preferred land cover classes - were inversely related to territory size but unrelated to pack size.

5. These results suggest that wolves in boreal ecosystems alter territory size, but not pack size, in response to local variation in habitat quality. This could be an adaptive strategy to balance tradeoffs between territorial defense costs and energetic gains due to resource acquisition. That

pack size was not responsive to habitat quality suggests that variation in group size is influenced by other factors such as intra-specific competition between wolf packs.

Keywords: anthropogenic disturbance, boreal forest, Brownian bridge, generalized least squares, optimal group size, predator density, repeated measures, rubber disc hypothesis, spatial autocorrelation, territoriality

Introduction

For carnivores there is often a strong positive relationship between density and habitat quality as defined by available prey biomass (Miquelle *et al.* 1999; Carbone & Gittleman 2002; Fuller, Mech & Cochrane 2003; Markar & Dickman 2005). Local density for a gregarious territorial species can be defined as the average territory size divided by average group size (Mosser *et al.* 2009), so higher densities could result from either metric.

Territory size is expected to be inversely related to habitat quality since the energetic costs associated with maintaining territories typically ensures they are as large as necessary, but as small as possible (Macdonald 1983). This implies a flexible approach to territoriality, the so-called rubber disc hypothesis first described by Huxley (1934). This has been observed in multiple carnivore species. For example, coyote (*Canis latrans*) group territory sizes contract with increasing hare and deer densities in Eastern Canada (Patterson & Messier 2001), leopard (*Panthera pardus*) home range sizes throughout Africa and Asia are inversely related to available prey biomass (Markar & Dickman 2005) and female lion (*Panthera leo*) home range sizes similarly decrease with increasing prey biomass in Zimbabwe, after accounting for pride biomass (Loveridge *et al.* 2009).

Alternately, if fitness is linked to habitat quality one might expect groups holding the best habitat to exhibit higher rates of reproduction and recruitment, logically contributing to greater potential for large group size, as seen in Serengeti lions (Mosser *et al.* 2009). Large lion prides out-compete smaller prides for high quality habitat (Mosser 2008) and patch richness has been demonstrated to determine maximum lion group biomass (Valeix, Loveridge & Macdonald 2012). European badger (*Meles meles*) group size has also been shown to positively correlate with patch quality, as measured by earthworm abundance (Kruuk & Parish 1982). Furthermore, the rate of emigration from social groups can be inversely related to resource availability as mediated by intra-specific competition (Bowler & Benton 2005; VanderWaal, Mosser & Packer 2009). This potentially results in lower emigration rates from better quality habitat (Stacey & Ligon 1987; Pasinelli & Walters 2002) leading to increased group sizes therein. Although habitat quality is most often, and directly, expressed as food availability (Carbone & Gittleman 2002) other measures of quality include available shelter (Sprent & Nicol 2012), level of disturbance (Kapfer *et al.* 2010), vegetative cover (McLoughlin *et al.* 2003) and proportion of open water (Fortin, Blouin-Demers & Dubois 2012).

Here we use GPS radio-telemetry for 34 wolf packs in northern Ontario to determine which environmental factors most influence winter wolf space use across a boreal forest ecosystem. We then employ the projected wolf use probabilities, habitat attributes identified as disproportionately utilized by wolves and an independent prey abundance measure, as quality metrics to test whether local variation in wolf population density results from adaptive changes in pack size or territory size. If wolves respond to changes in habitat quality behaviourally by adjusting their pack size to match local environmental conditions at the pack level, then we would expect to see habitat quality metrics positively related to pack size, whereas if wolves are

adjusting their territory size to match these conditions we would expect to see an inverse relationship between quality metrics and territory size.

Materials and Methods

Study area

Research was conducted in the boreal forest of Northern Ontario's Shield Ecozone between 92°1'W, 52° 6'N and 86°32'W, 49°49'N (Crins *et al.* 2009). Common trees include black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). Tamarack (*Larix laricina*) and white cedar (*Thuja occidentalis*) are restricted to lowland sites (Crins *et al.* 2009).

The study area straddles the northern boundary of the Ontario Ministry of Natural Resources' Area of the Undertaking (AOU), where timber extraction is licensed. Subsequently there is a marked southeast to northwest transition from high to low levels of anthropogenic disturbance, accompanied by a similar gradient in predator and prey densities. Wolf density estimates, derived from the total number of known individuals within the minimum convex polygon (MCP) of all telemetry re-locations, were 5.1/1000km² in the southeast and 3.1/1000km² in the northwest. Moose density, estimated from fixed-wing aerial surveys, was 46/1000km² in the southeast and 24/1000km² in the northwest. The spatial distribution of moose and wolves were sampled across this gradient, centred on the townships of Pickle Lake in the northwest and Nakina in the southeast.

Wolf resource utilization

Between February 2010 and January 2013 52 wolves were tracked using GPS telemetry collars (Lotek 7000MA, 7000SAW, Lotek Inc, Newmarket, Ontario); 37 individuals representing 23 packs in the southeast and 15 from 11 packs in the northwest (Fig. 1). Wolves were captured using padded leg-hold traps (#7 EZ grip, Livestock Protection Co., Alpine, Texas, USA) in summer (2010 – 12) and helicopter net-gunning in winter (2010-12). Summer captures were immobilized with a xylazine hydrochloride (2 mg/kg) and Telazol (4 mg/kg) combination with a Yohimbine (0.15 mg/kg) antagonist. Winter captures were physically restrained but not chemically immobilized during collaring. Wolf re-locations were recorded every 2.5- 5 hours with fix rate success averaging 91% (range 77-99%, n=17, Anderson 2012) allowing for unbiased resource utilization analyses (Frair et al. 2004).

Instead of averaging un-standardized coefficients from individual-level resource utilization functions to infer population-level processes (Marzluff *et al.* 2004, Long *et al.* 2009) we developed population-level utilization distributions (UDs) for winter (1 November – 30 April) which were linked directly to landscape characteristics. This allows for population-level patterns to be detected directly. Furthermore, because population-level UD were created by amalgamating individual pack-level UD, this method permits the effective incorporation of territoriality as well as individual variation in selection (Bolnick *et al.* 2003)

Pack-level utilization distribution

Utilization distributions were determined (cell size = 100x100m) for each individual/winter using kernel Brownian bridge (kbb) home range estimation (Calenge 2006). This is conditioned on the start and end spatial coordinates of each move, time between points

and the individual's speed of movement (Bullard 1999; Horne *et al.* 2007). Two smoothing parameters incorporated into the kbb model relate to each individual animal's mobility (σ_1) and relocation imprecision (σ_2). The R function *liker* (Horne *et al.* 2007) was used to estimate σ_1 , with σ_2 defined as 30m (Frair *et al.* 2010). Given the number and frequency of relocations used here, it is unlikely that utilization estimates substantially differ from those obtained using fixed kernel density estimation (Horne *et al.* 2007 Fig. 3). However an advantage of the kbb method, given its mechanistic basis, is that frequently used areas of an animal's range are more likely to be connected via pathways (Horne *et al.* 2007). For wide ranging species like wolves, selected movement paths influence prey availability and encounter rates (McPhee *et al.* 2012). Therefore it is useful to probabilistically estimate movements between observed locations, and objectively quantify and incorporate into estimates uncertainty resulting from the time and distance between these observations (Horne *et al.* 2007). This provides a more accurate assessment of the areas an individual actually used (Horne *et al.* 2007) and provisions greater allowance for unused areas of potential biological significance. It is important to note that this method is informative only when successive locations are autocorrelated (Kie *et al.* 2010) since as the relocation interval increases, the inherent assumption of a conditioned random walk with constant movement rate between relocations becomes less realistic (Horne *et al.* 2007). Autocorrelation is typical of fine scale temporal data generated by GPS telemetry and incorporating it into range utilization estimates instead of accounting for it by sub-sampling data is appealing.

Wolves move widely and rapidly through their ranges, often utilizing movement corridors along linear features (Whittington, Cassady St.Clair & Mercer 2005; Latham *et al.* 2011). This allows them to visit all parts of their range within 1-3 weeks (Weaver 1994;

Jedrejewski *et al.* 2001) and results in “holes” of low use within territories. Brownian bridge UD were therefore determined for all individuals with data covering >10% of the winter (18.4 days). Average coverage was 105 days (57.2%; N=62). A linear regression conducted with pooled data showed no relationship between number of fixes and range size ($P > 0.15$). If two pack-related individuals were tracked in a single winter but exhibited no temporal overlap, we calculated kbb UD for each and combined them with cell values weighted by relative temporal coverage (i.e. if wolf A was tracked for 25% of winter and wolf B 50%, wolf A’s values were weighted half those of wolf B’s in the combined UD (i.e. 0.33 and 0.67)). If two pack-related wolves overlapped in time, only the individual with the longer tracking duration was retained.

Landscape-level utilization distribution

Kernel Brownian bridge UD were converted to volume UD (vUD) for which the value of a pixel equals the percentage of the smallest home range containing it (Calenge 2006), therefore ascribing low values to high use areas (i.e. the vUD value is 10 for a pixel included in an animal’s 10% territory and 95 for a pixel included only in the 95% territory). The study area was overlaid with a grid of hexagonal cells, with 500m between centroids. Within each resulting 0.22km² hexagonal cell the average pack vUD value was extracted. Volume UD were subtracted from 100 to arrive at more intuitive measures for each cell (i.e. a cell with vUD of 95 was valued as $100 - 95 = 5$). Only hexagons with values > 5 were retained to mimic the 95% territory. Individual pack use values were integrated to 1 to remove bias imposed by differing territory sizes. If multiple pack ranges overlapped single cells, values were summed to determine the cumulative use of cells. This was repeated to create 4 landscape-level winter wolf UD (2009-10

to 2012-13). The final population-level UD_s were based on 60,196 relocations from 23 southeast and 11 northwest packs.

Statistical modeling of wolf UD

Each hexagon/year was associated with wolf use estimates from the relevant population level UD and with temporally appropriate habitat and landscape covariates. Relative elevation reflects the effect of localized topographical differences (i.e. highlands vs. lowlands) which influence dominant vegetation and can be meaningful to animal space use patterns (Kittle *et al.* 2008). We therefore calculated elevation at each pixel's centroid relative to the average elevation within a 500m radius buffer calculated from a digital elevation map (NASA Land Processes Distributed Active Archive Centre (LP DAAC) 2009). Current and preceding seasons' average normalized difference vegetation indexes (NDVI) were also calculated, indicating vegetation growth across the landscape (NASA Land Processes Distributed Active Archive Centre (LP DAAC) 2013). These were determined by averaging the 250m resolution, 16-day windows that cover the relevant season's 4-month core (June-September for summer and December-March for winter). This provides a generic measure of vegetation growth, as opposed to standing biomass (Pettorelli *et al.* 2005), that complements individual land cover classes and may be used as a cue by wolves in their search for prey (Courbin *et al.* 2014). Independent variables also included Boolean measures of proximity to dump (<1km=1; >1km=0), settlement (<1km=1; >1km=0), primary (paved and primary classes) roads (<500m=1; >500m=0) and secondary roads (secondary, tertiary, rail and utility classes) (<500m=1; >500m=0). Dumps provide a spatially fixed and consistent food source for wolves to exploit (Ciucci *et al.* 1997; Lesmerises, Dussault

& St-Laurent 2012) whereas settlements can represent heightened risk and have been used as spatial refugia by herbivores to avoid wolves (Hebblewhite *et al.* 2005). Roads, which can increase mobility and lead to improved hunting efficiency (James & Stuart-Smith 2000; Whittington *et al.* 2011), are selectively used as travel corridors where vehicle traffic is sparse (Hebblewhite & Merrill 2008). Similarly, shorelines can provide increased mobility for wolves and may provision increased encounters with prey (Latham *et al.* 2011), so distances (km) to shorelines of rivers or large lakes (>500m in diameter) were also included. Unlike roads, dumps and settlements, these features are widely distributed across the landscape so Boolean conversion was unnecessary.

Land cover proportions were calculated for each cell using the 30m² resolution Far North Land Cover map (OMNR 2013). This map does not extend south of ~50° N latitude so was merged with an earlier Ontario Land Cover map (Spectranalysis Inc. 2004) where necessary. Maps included updated disturbances (fire and harvest) for each year of the study. Land cover classes were amalgamated into 9 categories. These included water (open and turbid classes) which offers the possibility of increased prey vulnerability in winter (Kunkel & Pletscher 2001). Lowland classes, typically avoided by wolves in winter (McLoughlin *et al.* 2003), were defined as open lowland (open fen, open bog and freshwater marsh classes), treed lowland (treed peatland, treed fen, treed bog and coniferous swamp classes) and deciduous lowland (thicket swamp and deciduous swamp classes). Deciduous (deciduous treed class) and mixed upland (25-75% deciduous and 25-75% coniferous; mixed treed class) classes represent preferred moose forage (Peek 2007) whereas sparse forest (sparse treed class) is preferred by woodland caribou (*Rangifer tarandus caribou*), the secondary prey species of wolves in this system (O'Brien *et al.*

2006). Disturbed (disturbed treed/shrub and disturbed non/sparse classes representing natural and anthropogenic disturbances) classes, typically preferred by moose for forage (Brown 2011), were differentiated from newly disturbed (< 1 year from fire or forestry disturbance) classes. A 10th category, coniferous forest, considered the default of the boreal and highly correlated with the other land cover classes (Dormann *et al.* 2013), was withheld from the model as the reference class in comparison to which other classes were interpreted (Hosmer & Lemeshow 2000).

A total of 169,738 hexagonal cells were thus characterized. Due to computational constraints a single analysis of the dataset was impossible so hexagons were systematically sub-sampled at every 50th location from west to east starting from the NW corner (Long *et al.* 2009).

This was repeated 49 times with the second sub-sample starting from the 2nd hexagon from the NW corner, then from the 3rd, then the 4th until all hexagons were sampled. This ensured no hexagons were repeated in any of the 50 sub-samples. After conducting correlation analysis to ensure independent variables were not highly correlated ($r < 0.7$; Dormann *et al.* 2013), 50 generalized least squares (GLS) mixed effect regression models (gls in R package nlme), one for each sub-sample, were used to link wolf use to the full suite of predictor variables. The natural logarithm of the wolf use value was used to better fit model assumptions. GLS models allow spatial autocorrelation in the response variable to be explicitly accounted for as random effects (Zuur *et al.* 2009). Using GLS two additional parameters, the spatial autocorrelation range and nugget, are estimated. The range is a distance measure indicating the point on the x-axis of a variogram at which autocorrelation between points disappears, whereas the nugget is the y-value when the distance between points is 0, and represents the variable discontinuity imposed by the spatial structures at distances less than the actual minimum distance between points (Zuur *et al.*

2009). These random effects are meant to improve parameter estimate precision by separately modelling the dependence structure between measurements which otherwise gets incorporated into parameter estimates (Zuur *et al.* 2009). Semi-variograms of normalized residuals were employed to initially detect autocorrelation and inform initial range and nugget estimates (Crawley 2007). Rational quadratic spatial correlation (corRatio in nlme) dealt most effectively with the spatial autocorrelation in response variables, determined by comparing various correlation structures using AIC and visualizing output with semi-variograms of normalized residuals (Crawley 2007). Plots of normalized residuals against fitted values and normal plots were used to verify model fit (Crawley 2007).

Output model coefficients were averaged among the 50 models and all predictor variables retained. This method includes the uncertainty inherent in the models based on the logic that effects that vary substantially in direction among the 50 subsamples should average out to ~0 (Harrell 2001; John Fieberg, University of Minnesota, personal communication). An additional benefit of running 50 separate models was that it allowed for the empirical estimation of confidence intervals. The averaged coefficients from the model output were then used to project wolf use values across the landscape.

Mean confidence intervals were determined for each model-averaged coefficient using:

$$\hat{\beta} \pm (z_{\alpha/2}) * (\sigma / \sqrt{n})$$

where $\hat{\beta}$ = model averaged coefficient estimate, $z_{\alpha/2}$ = 95% critical value of the normal distribution, σ = standard deviation of coefficient estimates (β) across all models and \sqrt{n} = square root of total number of coefficient estimates (β).

Comparing quality metrics to individual pack characteristics

Pack size was enumerated during winter/spring helicopter captures when most wolves were collared and packs typically range as a cohesive unit (Mech & Boitani 2003). Pack size was further monitored during winter kill site investigation and collar retrieval when numbers were estimated from the number of beds around kills and backtracking to open areas (e.g. frozen lakes) where packs fanned out and individual tracks could be counted. This often allowed multiple pack size estimates which were averaged to provide a single mean seasonal estimate. Range attributes of collared individuals travelling alone were excluded from analysis. These “satellites” tend to be motivated by different factors than pack living animals, such as searching for mates or territory, and display different spatial patterns as a result, typically roaming widely across the landscape (Mech & Boitani 2003). Using only packs >1 with pack size directly determined in the field in the same winter as data collection resulted in 42 winters of data from 26 different packs.

The size of each pack’s 95% territory and 50% core area were determined from the Brownian bridge kernels and, using known pack sizes, local density of each was determined. Measures of habitat quality were then determined for these same 95% territories and 50% core

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areas (Table S1, Supporting material). These were the average projected wolf use value, the probability of moose occupancy of each pixel (Lele *et al.* 2013) as projected from an independent resource selection probability function analysis (Street *et al.* unpublished manuscript; a description of the resource selection modelling procedure is detailed in Appendix S1, Supporting material), and the proportion of individual land cover variables selected or avoided by wolves in the population-level model. These were considered measures of habitat quality because areas of higher projected wolf use, which emerged from the population-level resource utilization analysis described above, reflects population-level wolf habitat selection that over evolutionary time, should maximize fitness (Morris 2003). Following this logic, specific habitat classes selected at the population level were defined as high quality and those avoided as low quality. Areas of higher probability of moose occupancy reflect better habitat in that it is more likely to hold prey resources, a key factor influencing predator distribution and abundance (Carbone & Gittleman 2002). Since individual pack characteristics were measured across multiple years, repeated measures linear mixed effects modeling was employed to investigate the link between these quality measures and local wolf density, pack sizes and territory sizes. The influence of pack size on territory size was similarly assessed at both 95% and 50% levels. Pack size, territory size and wolf density were each log transformed to better meet modeling assumptions.

Statistical and spatial analysis was undertaken using R software version 2.15.1, R Development Core Team 2012, ArcMap 10.1 (ESRI Inc.) and Geospatial Modeling Environment 0.7.2.0.

Results

Wolves tended to use lower elevation areas relative to the immediate surroundings but also avoided both open and treed lowlands (Fig. 2). Deciduous, mixed and disturbed forest areas were preferentially utilized whereas recently disturbed areas were avoided. Open water was similarly avoided whereas areas close to shorelines were strongly selected (negative coefficient for increasing distance). Associations with anthropogenic features were mostly positive, with dumps strongly selected, settlements eliciting no strong response and areas close to roads, particularly secondary roads, preferentially used. Vegetation growth, as measured by NDVI, was influential and associations indicated use of areas with low winter growth (negative β) but high summer growth (positive β).

Wolf densities within the 95% and 50% territories exhibited consistently positive associations with habitat quality metrics (Table 1). Local wolf density was strongly correlated with wolf use as projected from the GLS model and was also positively associated with average probability of moose occupancy (Fig. 3). Mixed forest proportion was also positively associated with local wolf density (95%: $R^2 = 0.26$, $P < 0.01$; 50%: $R^2 = 0.18$, $P < 0.05$). The proportion of disturbed forest showed a similar trend but the relationship was marginally significant only at the 95% range ($R^2 = 0.04$, $P < 0.1$). Conversely the open lowland proportion was negatively associated with wolf density, weakly so within the core range (95%: $R^2 = 0.21$, $P < 0.01$; 50%: $R^2 = 0.14$, $P < 0.1$).

Territory size was also consistently associated with most measures of habitat quality (Table 1). Larger 95% and 50% territories had lower average projected wolf use values and also had lower average moose occupancy probabilities (Fig. 4). Larger ranges also included lower

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mixed forest proportions at both scales (Table 1; 95%: $R^2 = 0.14$, $P < 0.05$; 50%: $R^2 = 0.09$, $P < 0.1$) as well as lower proportions of disturbed forest (95%: $R^2 = 0.17$, $P < 0.01$; 50%: $R^2 = 0.03$, $P \leq 0.1$) although in both instances associations with core territories were weak. Open lowland was positively associated with the 95% range size ($R^2 = 0.22$, $P < 0.01$) indicating that larger ranges include proportionally more of this poor quality habitat. The proportion of deciduous forest (high quality) was not associated with local density or territory size ($P > 0.1$). In comparison, there was no significant relationship between pack size and any of the habitat quality variables tested (Table 1). We found no significant relationship between territory size and pack size at the 95% level ($P = 0.17$) and a marginally positive relationship at the 50% core ($P = 0.09$).

Discussion

Wolf resource utilization across this broad, heterogeneous landscape was influenced by a variety of landscape modifiers and habitat attributes. Wolves made disproportionate use of deciduous, mixed and disturbed forest, corresponding to high quality moose habitat (Peek 2007; Brown 2011; Street *et al.* unpublished manuscript). Conversely, lowland habitat was avoided here, as in other boreal sites elsewhere in Canada (McLoughlin *et al.* 2003), as were frozen lakes. However, wolves heavily used shorelines, which are typically preferred as travel corridors (Latham *et al.* 2011). Anthropogenic disturbances were generally exploited. Dump sites were disproportionately utilized as expected given that they were situated away from settlements and therefore represent a consistent and largely risk-free food source (Murray *et al.* 2010). Areas close to roads were also preferred. Like shorelines, sparsely used transport corridors provide a

convenient means for wolves to move quickly through the landscape (Hebblewhite & Merrill 2008; Latham *et al.* 2011). This increase in velocity across the landscape has been linked in this system to higher kill rates of moose by wolves (Moffatt 2012). Such linear features can also be important for territorial behaviour, used as territorial boundaries via scent marking (Peters & Mech 1975).

Direct fitness measures such as demographic vital rates should be ideal indicators of habitat quality (Van Horne 1983) but such basic measures as reproductive rate are often density-dependent, complicating habitat assessment for a population near its ecological carrying capacity (Mitchell & Hebblewhite 2012). More problematic is that accurate fitness measures are difficult to attain (Silk 2007). As a result density is often used as an indicator of quality given its intuitive link with fitness (McLoughlin *et al.* 2010). For territorial species where social restrictions on access to prime habitat increases the chances of subdominant individuals or social groups utilizing suboptimal habitat (Fretwell & Lucas 1969), the putative relationship between habitat quality and density may be obscured (Van Horne 1983; Mosser *et al.* 2009; DeCesare *et al.* 2014). However, even in species not under ideal free distribution, density can provide a better short term measure of habitat quality than demographic vital rates due to environmental and demographic stochasticity (Mosser *et al.* 2009). Given these complications, demonstrating a clear link between density and habitat quality is particularly useful for population management. Here local wolf density was positively related to probability of moose use, consistent with observations that the main factor driving obligate carnivore densities is the density or availability of prey (Fuller & Sievert 2001; Carbone & Gittleman 2002; Fuller, Mech & Cochrane 2003; Karanth *et al.* 2004). Consistent relationships between pack-level density and the other habitat

quality metrics here further suggests that local density may be a reasonable metric of short-term habitat quality in this system (Mosser *et al.* 2009, van Beest *et al.* 2014).

In a seminal paper Macdonald (1983) demonstrated a strong positive correlation between wolf pack and territory sizes, as well as a similar relationship between coyote, lion and spotted hyena (*Crocuta crocuta*) groups and their territories. However more recent studies have typically failed to find such a relationship for coyotes (Patterson & Messier 2001) or wolves (Potvin 1988; Fuller 1989; Mech *et al.* 1998) and in Montana, wolf territory sizes were inversely correlated with pack size (Rich *et al.* 2012). Lions in the Selous showed no relationship between group and territory size (Sprong 2002) whereas Serengeti lions did, albeit only when partitioned by habitat type (Mosser & Packer 2009). Large spotted hyena clans in Ngorongoro Crater held larger territories than did smaller clans (Höner *et al.* 2005). The relationship between group and territory size can be nuanced such as for Ethiopian wolves (*Canis simensis*) for which territory size is primarily determined by the number of adult males plus the dominant female in a group, not the group size as a whole (Tallents *et al.* 2012).

Maintaining a territory requires considerable energy expenditure to enable perimeter patrol, scent marking and occasional direct aggression against transgressors, so it should therefore be big enough to encompass essential resources, but small as possible to ensure energetic efficiency (Macdonald 1983). This results in the oft-observed inverse relationship between territory size and habitat quality (Gass, Angehr & Centa 1976; Village 1982; Smith & Shugart 1987; Mills & Knowlton 1991; Patterson & Messier 2001; McLoughlin *et al.* 2003;

Markar & Dickman 2005; but see Tallents *et al.* 2012). This pattern was also detected in our study suggesting that wolves here employ an adaptive approach to territoriality, whereby the extent of the defended core shifts as a function of resource quality, consistent with the elastic disc hypothesis (Huxley 1934; Potts, Harris & Giuggioli 2013). This strategy allows wolves to optimize the trade-off between the costs of territorial defense and gains from resource acquisition (Hixon 1980; Schoener 1983).

Pack size was not linked with any available metrics of habitat quality at either scale, including prey habitat preference, indicating that wolf group size is regulated by other factors. Optimal group size theory indicates that territorial animals should strive to best compromise the potential advantages of shared costs vs. disadvantages arising from resource depletion (Brown 1982). Larger foraging groups often have improved attack success and are able to subdue larger prey, broadening their available prey base (Creel & Creel 1995). However large groups do not necessarily confer foraging advantages (Schmidt & Mech 1997) because the cost of sharing the spoils (Packer, Scheel & Pusey 1990), tendency to “free ride” (MacNulty *et al.* 2012) and reduced efficiency of group search can outweigh any potential benefit (Caro 1994; Fryxell *et al.* 2007). The optimal foraging group size for wolves based on per capita intake has been estimated at ~2 (Thurber & Peterson 1993; Hayes *et al.* 2000) although offsetting the impact of scavenging by ravens (*Corvus corax*) might promote formation of larger groups (Vucetich *et al.* 2002). Similarly, small group size was predicted for African wild dogs (*Lycaon pictus*) until variation in foraging costs were incorporated into the determination of energetics of cooperative hunting, which increased the pack size predicted by peak per capita food intake rate (12-14) such that it closely matched the modal observed adult pack size (10) (Creel & Creel, 1995).

An alternative mechanism promoting increased pack size is intra-specific competition, including protection of young from con-specific predation (Packer, Scheel & Pusey 1990). Larger lion prides dominate smaller ones (McComb, Packer & Pusey 1994; Heinsohn & Packer 1995) and are significantly more able to control disputed areas and improve their territory quality through acquisition of additional area (Mosser & Packer 2009). In highly competitive environments, retaining group members might be even more important (Heinsohn 1997). For example, where overall lion density was high, females were less likely to disperse from prides surrounded by large numbers of unrelated females than would be predicted based on the habitat's ability to sustain them (VanderWaal, Mosser & Packer 2009). Similarly, Rich *et al.* (2012) found an inverse relationship between wolf territory size and both pack size and intra-specific competition as measured by density of packs (not wolves), indicating a positive correlation between pack size and competition. However an inverse relationship between territory size and forest cover, indicating habitat quality, was also observed so whether larger pack size was a response to increased pack density (i.e. competition) or whether both factors were by-products of higher quality habitat is uncertain. These uncertainties expose the gaps that exist in the chain of evidence linking social behaviour in mammals to fitness outcomes (Silk 2007). Our results exhibit no direct support for the hypothesis that wolf group size is influenced by intra-specific competition, but the absence of any correlation with habitat quality elevates the potential of this hypothesis by eliminating one alternative (response to habitat quality).

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Data Accessibility

Relevant data is accessible as Table S1 and Appendix S1 in Supporting material. Table S1 is also archived in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.b21q1> (Kittle et al. 2015).

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Tables

Table 1: Summary of linear regressions of individual level pack attributes against un-weighted population model projection of wolf use, probability of moose occupancy and proportion of range comprised of habitat variables selected or avoided by population-level model. Analyses at the 95% territory and 50% core territory are shown (N = 42).

Habitat quality variable	Density		Range Size		Pack Size	
	95%	50%	95%	50%	95%	50%
Projected wolf use	(+)*	(+)**	(-)**	(-)**	NS	NS
Probability of moose occupancy	(+)	(+)*	(-)**	(-)**	NS	NS
Proportion deciduous forest	NS	NS	NS	NS	NS	NS
Proportion mixed forest	(+)**	(+)*	(-)*	(-)	NS	NS
Proportion disturbed forest	(+)*	NS	(-)**	(-)	NS	NS
Proportion open lowland	(-)**	(-)	(+)**	NS	NS	NS

NS= not significant, () = $P \leq .1$, ()* = $P \leq .05$, ()** = $P \leq .01$, ()*** = $P \leq .001$

Figure Legends

Figure 1: Map of study area showing extent (bold line), location in Northern Ontario (inset) and water (grey) including the northeastern portion of Lake Nipigon (lower left). Ninety-five percent Brownian bridge home ranges for all wolf packs from winter 2010-11 are also shown indicating southeastern and northwestern sampling areas.

Figure 2: Averaged coefficient estimates (β) with mean 95% confidence intervals (CI) for un-weighted Generalized Least Squares resource utilization models (n = 50). Inset shows variables with relatively small coefficient values for clarity.

Figure 3: From 42 pack winters of 26 separate wolf packs, the 95% territory and 50% core area plots of log(wolf density) as a function of projected wolf use from un-weighted population level resource utilization model (95%: $R^2 = 0.43$, $P < 0.05$; 50%: $R^2 = 0.57$, $P < 0.001$), and as a function of probability of moose occupancy (“moose use”) from resource selection probability function (95%: $R^2 = 0.14$, $P < 0.1$; 50%: $R^2 = 0.18$, $P < 0.05$). Regression lines are shown (solid: $P < 0.05$; dotted: $0.1 < P > 0.05$).

Figure 4: From 42 pack winters of 26 separate wolf packs, the 95% territory and 50% core area plots of log(territory size) as a function of projected wolf use from un-weighted population level resource utilization model (95%: $R^2 = 0.50$, $P < 0.01$; 50%: $R^2 = 0.56$, $P < 0.001$), and as a function of probability of moose occupancy (“moose use”) from resource selection probability function (95%: $R^2 = 0.27$, $P < 0.01$; 50%: $R^2 = 0.22$, $P < 0.01$). Regression lines are shown.

Figures

Figure 1:

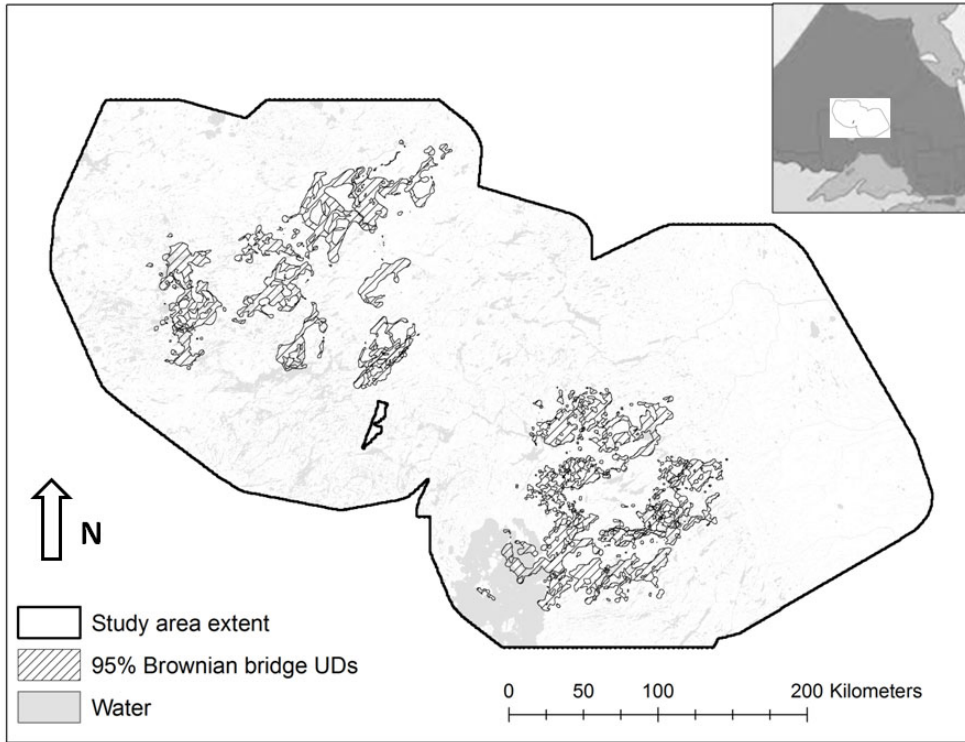


Figure 2:

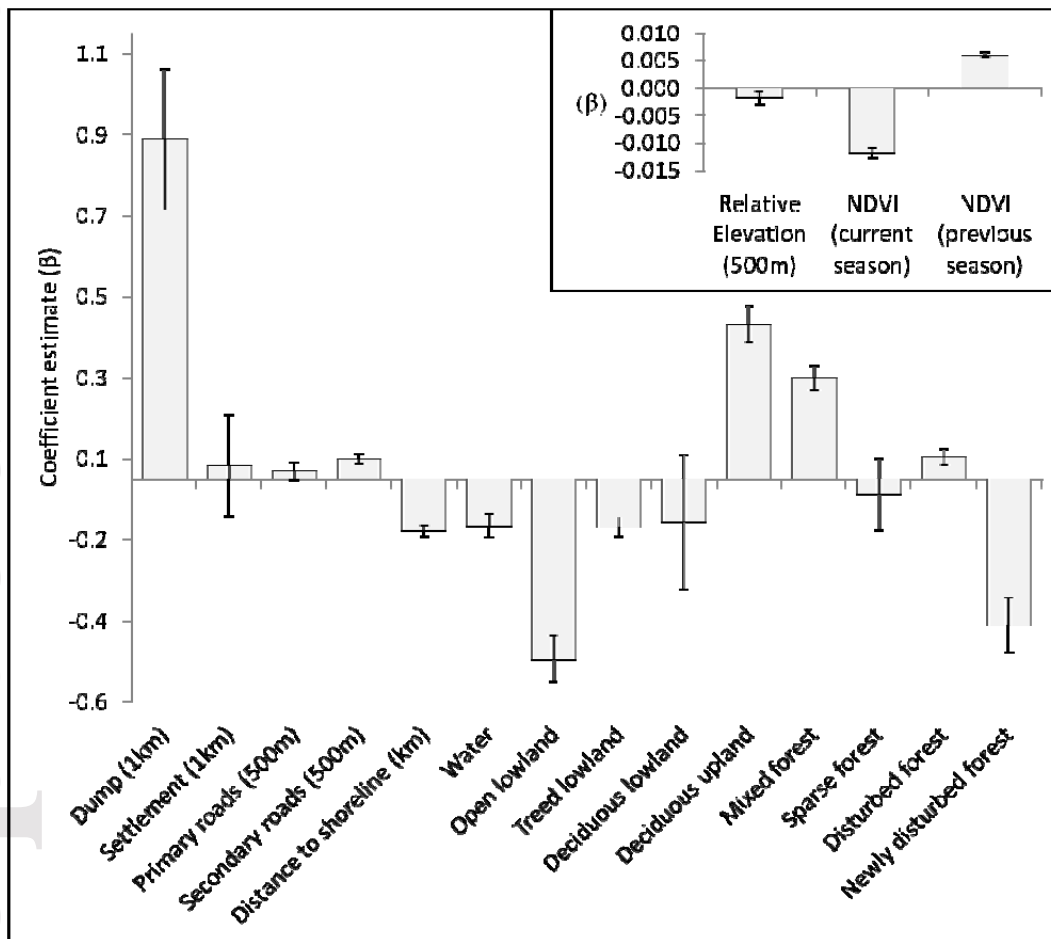


Figure 3

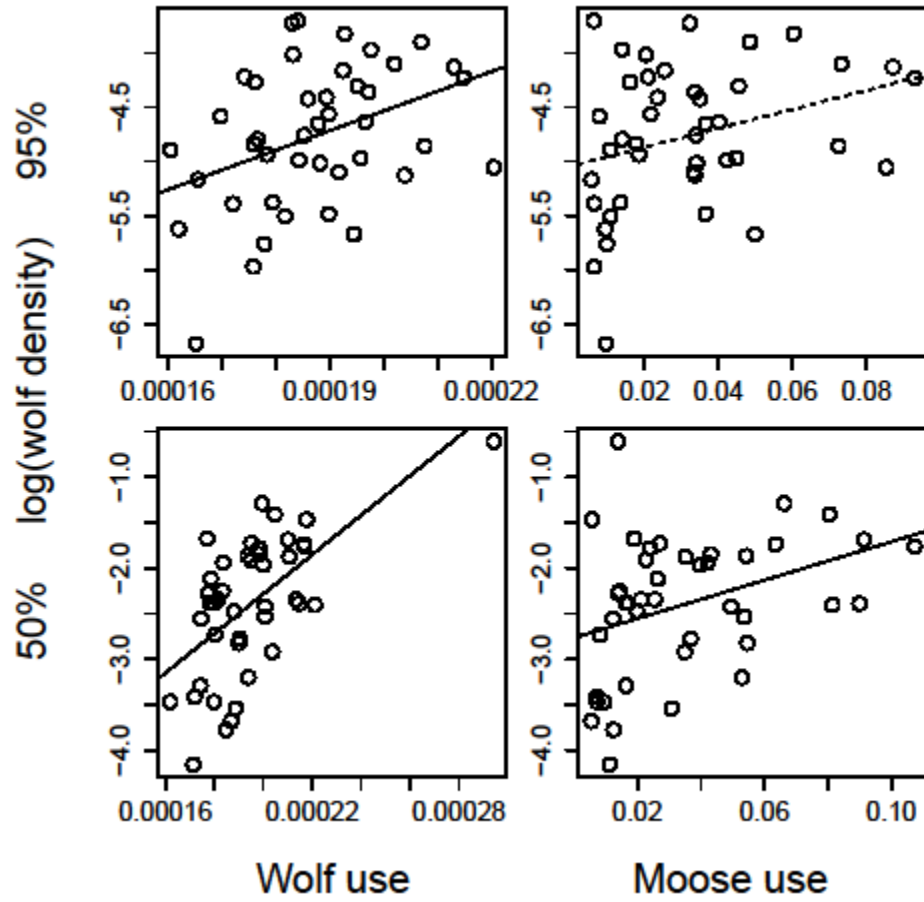


Figure 4

