

# Home-Range Size in Large-Bodied Carnivores as a Model for Predicting Neandertal Territory Size

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Adult human foragers expend roughly 30–60 kcal per km in unburdened walking at optimal speeds.<sup>1,2</sup> In the context of foraging rounds and residential moves, they may routinely travel distances of 50–70 km per week, often while carrying loads.<sup>3</sup> Movement on the landscape, then, is arguably the single most expensive item in the activity budgets of hunter-gatherers. Mobility costs may have been greater still for Neandertals. They had stocky, short-limbed physiques that were energetically costly to move<sup>4</sup> and lived in relatively unproductive Pleistocene environments<sup>5</sup> that may have required greater movement to deal with problems of biodepletion and resource patchiness.<sup>6</sup> But just how mobile were the Neandertals?

Among foragers, total mobility is a function of the frequency and aver-

age distances of residential moves (residential mobility), collecting and hunting trips away from camp (logistical mobility), and visiting trips to neighboring camps to satisfy social, reproductive, or other needs (social mobility). The frequency and distances of these types of movement are in turn related to the productivity and energy structure of ecosystems,<sup>6–8</sup> site settlement dynamics,<sup>9</sup> and population density,<sup>10</sup> none of which are currently well understood for Upper Pleistocene Europe. We may thus be some distance away from understanding the overall mobility of Neandertals, how it was partitioned between different types of movement, and how it varied relative to environmental and ecological conditions. However, we may be better able to estimate Neandertal home-range (territory) sizes. Doing so will have implications for understanding their total mobility and site settlement systems.

The question of Neandertal home-range size has most often been addressed through studies of the movement of lithic raw materials across space. In these studies, the maximum transport distances of discarded lithics from the flint outcrops from which the raw materials were

procured are generally taken, perhaps too simplistically,<sup>11</sup> as the radius of the home range of the group that made and used those lithics. Unfortunately, attempts to estimate home-range size from raw material movement have been applied only to a handful of Middle Paleolithic cases.

In deposits dated to Marine Isotope Stage (MIS) 5a at Baume-Vallée in south-central France, raw material movement suggests a potential territory of 6,644 km<sup>2</sup>. Lithic transport distances suggest a potential maximum territory area of 5,024 km<sup>2</sup> at the nearby MIS 3 site of Le Rond de Saint-Arcons.<sup>12</sup> Other studies have suggested larger home ranges. Flints from MIS 7-6 levels at Vaufrey and other sites in the Aquitaine Basin (France) suggest a territory of 13,000 km<sup>2</sup> for the Neandertals there.<sup>13,14</sup> In spite of the observation that the majority of flint at the MIS 3 Crimean site of Karabi Tamchin came from 25 km away, suggesting an approximate territory of only 1,962 km<sup>2</sup>, Burke<sup>15</sup> has argued that the Neandertals there would have needed the entire 27,000 km<sup>2</sup> of the Crimean peninsula to support an economy that depended heavily on the hunting of horses (*Equus hydruntinus*).

Raw material transport distances are typically larger in central and north-central Europe. In this region, flint movement generally suggests territory sizes on the order of 10,000 km<sup>2</sup> (for example, at Raj Cave in Poland and Kůlna in the Czech Republic<sup>14</sup>). The largest lithic-estimated territory size, however, comes from the Loire valley of

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central France, based on flints from the MIS 3 open-air site of Champ Grand. Ninety-nine percent of the lithics there were produced on local material procured within about 15 km, but exotic flints have been recovered from sources as far as 250 km to the north and 180 km to the south, effectively defining a catchment that encompasses much of central France.<sup>16</sup> Fitting a simple ellipse to the distribution of quarry sources for the exotic flint at Champ Grand produces a territory estimate of 54,000 km<sup>2</sup>.

Lithic-based estimates of Middle Paleolithic territory sizes are thus highly variable. The largest of these estimates are comparable to those of historically known Nunamiut Eskimo and Crow Indian groups (12,850–63,700 km<sup>2</sup>),<sup>17</sup> both of which lived at high latitudes and thus experienced cold-temperate conditions similar to Pleistocene Europe and relied primarily on hunting of terrestrial game (87% and 80% of total diet, respectively).<sup>17</sup> Does this variation in estimated Neandertal home-range sizes reflect something about Neandertal ecology and subsistence systems, perhaps reflecting variation in ecological productivity, or does it perhaps reflect problems with the assumptions underlying the estimation method?

Lithic transport estimates of territory size depend on the assumption that raw material procurement is embedded in subsistence mobility,<sup>18</sup> which is generally considered to have been the case in the Middle Paleolithic.<sup>19,20</sup> However, if the procurement of high-quality flint was logistically organized (that is, special trips were made to collect flint and transport it back to residential camps, as appears to have been the case in the Upper Paleolithic<sup>21,22</sup>), the movement of flint across the landscape might have little bearing on the size of the area exploited for subsistence or on the movement of Neandertals within that area. Exactly this kind of situation has been argued to have obtained during MIS 3 times in the Salento peninsula of southern Italy, where good-quality raw material is scarce and flint was imported by logistical forays to the

north.<sup>23,24</sup> In addition, raw material may have occasionally been traded between social groups or carried long distances by individuals visiting or migrating between groups. Accordingly, exotic flints may be informing us more about extraordinary movement or intergroup exchanges than about subsistence-based mobility.

While exotic flints that traveled 100–200 km can be found at many Middle Paleolithic sites, it is important to keep in mind that upwards of 98% of the lithics at these sites

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derive from sources within 15–20 km of camp,<sup>12,14,20,25,26</sup> which in turn might suggest more moderately sized territories. It is also possible that the generally high frequency of flint from local sources in Middle Paleolithic sites might reflect gender differences in raw material procurement, with the bulk of local flints having been collected by females during foraging rounds that were closer to camp, while the more exotic material came from collecting by males during more distant hunting forays.<sup>27–29</sup> If so, the movement of exotic flints may more accurately represent total territory size.

Might ecological relationships between productivity and home-

range size in historically known foragers provide a means by which to evaluate the lithic-based estimates? Unfortunately, various issues prevent us from following this avenue. Good-quality data on the territory sizes of hunters and gatherers are relatively rare, and those that do exist<sup>6,17</sup> (Fig. 1) reveal enormous variation among groups living in ecologically similar conditions. This variation primarily relates to dependence on aquatic resources. Neandertals did at times exploit aquatic resources, but never to the extent seen among high-latitude modern human foragers.<sup>3</sup> However, ecological relationships between productivity and home-range size in carnivores may provide some insights.

Across carnivores, home-range size varies positively with both body size and the proportion of meat in the diet.<sup>30</sup> In some carnivores, an inverse relationship between territory size and prey encounter rates has been documented.<sup>30,31</sup> These ecological relationships are played out in the empirical observation that, across the full range of carnivore body sizes, it takes a standing crop of 10,000 kg of prey to support 90 kg of carnivore.<sup>32</sup> Given a direct relationship between the biomass densities (kgs per unit area) of carnivores and their prey, and inverse relationships between prey biomass and carnivore home-range sizes, it stands to reason that detectable relationships must exist between the aggregate mass of a carnivore group, the biomass density of their prey, and their territory size. Neandertals appear to have been heavily reliant on meat, with diets comprised of between about 50%–90% animal tissue, depending on ecological circumstances.<sup>3</sup> Accordingly, the same sorts of ecological relationships would have been in play. However, we note that the need for hides may have significantly altered the relationship between Neandertal biomass and prey biomass relative to that of other carnivores.<sup>33</sup> We are operating here under the simplifying assumption that subsistence demands combined with carnivore competitive dynamics were the major determinant of Neandertal/prey biomass relationships.

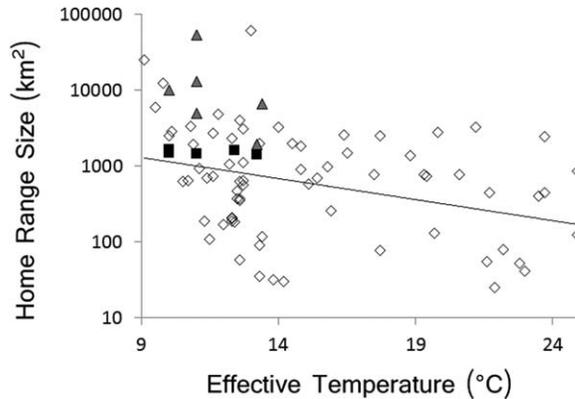


Figure 1. Home-range size ( $\text{km}^2$ ) versus effective temperature ( $^{\circ}\text{C}$ : as a measure of overall productivity) in recent hunter-gatherers (open diamonds: data from Kelly<sup>6,17</sup> and Binford<sup>2</sup>) and Neanderthals. Neanderthal home ranges were estimated using either lithic raw material transport distances (gray triangles) or models based on wolf ecology (black squares). Line represents an exponential regression,  $y = 4090.0^{-0.128x}$ ,  $r = -0.316$ .

Grey wolves (*Canis lupus*) share many ecological features with Neanderthals, and thus may make a good model for investigating Neanderthal mobility.<sup>34</sup> Wolves have a varied diet, but one that is heavily meat-dependent and focused on large ungulates. (Plant matter does not appear to be a significant component of wolf diets, although volumes approaching 10% have been documented in wolf guts<sup>35,36</sup> and scat.<sup>37,38</sup>) Like Neanderthals, wolves occupy cold temperate environments, have wide habitat tolerances, range widely, are capable of endurance locomotion, are social animals with flexible social structures, and regularly engage in cooperative hunting. Grey wolf territory size is also highly variable, ranging from just a few square kms to tens of thousands of square kms.<sup>39</sup> This affords us the opportunity to explore ecology-territory size relationships.

Walker and Churchill<sup>40</sup> used data on wolf territory size ( $\text{km}^2$ ), prey biomass ( $\text{kg km}^{-2}$ ), latitude ( $^{\circ}\text{N}$ ), average winter temperature ( $^{\circ}\text{K}$ ), and average winter precipitation (mm) from 104 wolf packs to explore variation in wolf territory size. The aggregate mass of wolf packs (in kg, calculated by multiplying pack size by the average mass of adult wolves in the region under study) was used as a measure of consumer demand. Multiple regression analysis showed strong intercorrelation between the ecological variables; the data best fit

a two-variable model using just aggregate mass and mean winter temperature.

The resulting regression equation was used to predict home-range sizes for Neanderthal social groups of roughly 10–11, 19–23, and 29–33 individuals during interstadial (MIS 3) and cold (MIS 6 and 4) conditions in southern France and the Crimea.<sup>40</sup> Predictions for Poland during interstadial and cold conditions were added later<sup>3</sup> to provide a greater number of comparisons with the lithic-based territory size estimates. When applied to Pleistocene climatic conditions,<sup>41</sup> the wolf model suggested that Neanderthals required and maintained territories of moderate size (ca. 1,400–5,400  $\text{km}^2$ ). These home ranges, like those estimated on the basis of lithic raw material transport, are large relative to the home ranges of most tropical foragers using predominantly circulating<sup>42</sup> settlement systems. They are large relative even to those of most mid-latitude groups for whom data are available, yet small compared to logistically organized arctic and sub-arctic groups (Fig. 1).

The wolf model, as applied to Neanderthals, implies territories with radii on the order of 20–40 km, which is consistent with the distances (15–20 km) that the majority of flint at Middle Paleolithic sites tended to be procured. This may lend support to the assumption that raw material procurement was

embedded in the subsistence rounds of Neanderthal groups: The preponderance of local flints may reflect the collection of raw materials during hunting or gathering trips within the “foraging radius” of the sites.<sup>20,43</sup> At some times and in some places, however, they may have scheduled flint procurement separately from subsistence rounds.<sup>23,24</sup> The markedly less frequent occurrence of exotic flints may reflect the movement of some curated tools during residential moves, logistical excursions, or social visiting.

While the predictions generated from the wolf data are largely concordant with estimates based on lithic transport, in no cases did the model predict home ranges of the sizes estimated from flint movement in the Aquitaine basin during MIS 7-6 (13,000  $\text{km}^2$ ),<sup>13</sup> north central Europe during MIS 4-3 (10,000  $\text{km}^2$ ),<sup>14</sup> or central France during MIS 3 (54,000  $\text{km}^2$ ).<sup>16</sup> This raises the possibility that the wolf-based estimates are too small. The wolf data derive in large part from places where wolves have little competition from other carnivores, although some data come from places where wolves compete with brown bears. Territorial exclusion and inverse density relationships exist between many competing carnivore species,<sup>44–47</sup> so that modern wolves may be able to subsist on smaller territories than would be possible if they faced heavier competition. Given that Pleistocene Europe hosted a rich carnivore guild,<sup>3</sup> competition with cave lions, cave hyenas, brown bears, wolves, dholes, and leopards may have meant that Neanderthals required more space per unit of body mass to satisfy their subsistence demands than do modern wolves.

To explore the effects of intraguild competition, we collected data from the literature on four sympatric African carnivores, including lions (*Panthera leo*) from thirteen study sites,<sup>48,49</sup> spotted hyenas (*Crocuta crocuta*) from thirteen sites,<sup>50–53</sup> cheetahs (*Acinonyx jubatus*) from ten sites,<sup>54</sup> and wild dogs (*Lycaon pictus*) from eight study sites.<sup>55</sup> Although sub-Saharan African ecology is very different from that of Pleistocene

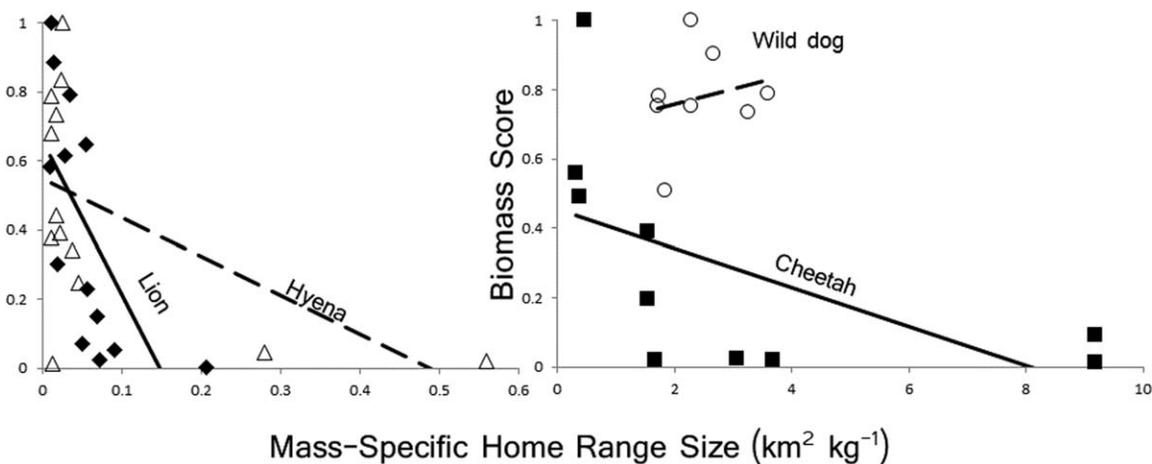


Figure 2. Mass-specific home-range sizes versus relative prey biomass in four sympatric African large-bodied carnivores. Mass-specific home-range size is the amount of area ( $\text{km}^2$ ) required to support 1 kg of carnivore. Biomass score is the amount of prey biomass at each site as a percentage of the biomass of the site for that species of carnivore with the highest amount of biomass. Ordinary least square regression lines: lion (black diamonds),  $y = -4.0108x + 0.0145$ ,  $r = 0.6271$ ; hyena (open triangles),  $y = -1.0863x + 0.0114$ ,  $r = 0.5359$ ; cheetah (black squares),  $y = -0.0731x + 9.1912$ ,  $r = 0.5993$ ; wild dog (open circles),  $y = 0.0720x + 3.2632$ ,  $r = 0.3157$ .

Europe, Africa provides the best example in the modern world of a multi-species guild of large-bodied carnivores (noting that the purpose of this exercise is to explore the effect of social dominance rank on relative home-range size, not to try to predict home-range sizes from African carnivore data). For each species, we recorded home-range size in  $\text{km}^2$  (for cheetahs, we took the inverse of population density as our measure of home-range size), group size ( $n$ ), and prey biomass ( $\text{kg km}^{-2}$ ). To compare across species having varying body mass and group sizes, home-range size (in  $\text{km}^2$ ) was divided by aggregate mass (in kg: taken as group size times average combined-sex adult mass<sup>56</sup>) to produce a mass-specific home-range size (in  $\text{km}^2 \text{kg}^{-1}$ ); that is, a measure of the area required to support 1 kg of carnivore. In the literature, prey biomass values were calculated in different ways for each species, making direct comparisons across taxa difficult. We thus converted estimates of prey biomass to biomass scores by dividing the estimate at each site by the site with the highest biomass for that species. Thus, for example, a lion site with a biomass score of 0.62 has a prey biomass that is 62% of the lion site with the highest density. No effort was made to differentiate guarded from

unguarded territories because defense of territories can vary within species<sup>57</sup> and our data sources generally did not note whether or not a home range was defended.

Two things are apparent when prey biomass is examined relative to mass-specific home-range size (Fig. 2). First, more space, by two orders of magnitude, is required to support a kilogram of cheetah or wild dog than a kilogram of lion or hyena. It takes, on average, 5.5 ha ( $\pm 5.2$  ha) to support a kilogram of lion and 8.3 ha ( $\pm 16.0$  ha) per kilogram of hyena, while it takes an average of 310.1 ha ( $\pm 339.3$  ha) per kilogram of cheetah and 242.1 ha ( $\pm 70.5$  ha) per kilogram of wild dog. Lions and spotted hyenas are “behaviorally dominant” (or “socially dominant”; that is, more likely to prevail in direct aggressive interactions and more likely to spatially exclude competitors) over wild dogs and cheetahs.<sup>44,58,59</sup> While guilds of large carnivores annually remove about 15% of all available prey, the dominant species in the guild may monopolize up to two-thirds of that take, leaving the less dominant species to compete for the remaining third.<sup>60</sup> Lions appear to be the ranking members of the African large-bodied carnivore guild. Not surprisingly, they constitute about half of the biomass at their trophic level.<sup>3</sup> These dominance relation-

ships are played out in terms of foraging mobility: Wild dogs and cheetahs must cover relatively more ground to satisfy their metabolic demands because of the competition they experience from hyenas and lions.

Second, species vary in relationships between prey biomass and their need for space. Lions evince a strong and significant ( $p = 0.029$ ) negative relationship between biomass score and relative home-range size: As prey biomass decreases, lions need slightly more space to satisfy demand (Fig. 2). Similar relationships hold for hyenas and cheetahs, although the slopes are not as steep, meaning that these species require relatively more space per unit mass than do lions as prey biomass decreases. (Note, however, that the slopes do not quite reach significance in either species:  $p = 0.072$  for hyenas,  $p = 0.073$  for cheetahs). Wild dogs, on the other hand, appear to show a positive relationship between prey biomass and home-range size (Fig. 2). Unfortunately, the observed relationship is not statistically significant ( $p = 0.490$ ), but a positive correlation between these variables is not unexpected. Wild dogs tend to do worse in areas of high prey density because, while kill rates may go up in those areas, lions and hyenas tend to be more

abundant there, so that more carcasses are lost to these larger, more aggressive competitors.<sup>61,62</sup>

These data from African carnivores, scant as they are, suggest that competition has a strong effect on the relationship between secondary productivity and home-range size. This raises the distinct possibility that the size of Neandertal home ranges may have been partially determined by the dynamics of competition with large-bodied carnivores.<sup>3</sup> Mass-specific home ranges of wolves (using data from Walker and Churchill<sup>40</sup>) vary between 275.0 and 362.9 ha kg<sup>-1</sup>. This is comparable to the home ranges of cheetahs and wild dogs, despite the fact that wolves suffer much less competition than do African carnivores. The relatively large home ranges of wolves is likely a function of the lower productivity, and hence lower overall prey biomass, of the boreal forest and tundra environments from which most of the data derive.

Estimates of moderate-to-large sized prey biomass for high latitude ecosystems tend to be an order of magnitude lower than those of African savannah ecosystems (high latitude median = 274 kg km<sup>-2</sup>, range = 10–1,655 kg km<sup>-2</sup>, n = 27; African savannah median = 3,783 kg km<sup>-2</sup>, range = 984–11,576 kg km<sup>-2</sup>, n = 21).<sup>2</sup> Not surprisingly, even apex predators have to range much more widely to find prey at higher latitudes. The lower end of the lithic-based home-range estimates for Neandertals equate with mass-specific territory sizes of 334.9–1,328.8 ha kg<sup>-1</sup>, assuming aggregate masses of Neandertal social groups to have been between 500–1,500 kg,<sup>40</sup> which, at the lower end at least, overlap the values observed for modern wolves. Lithic-based estimates would mean mass-specific home-range sizes of 666.7–10,800.0 ha kg<sup>-1</sup>, again assuming aggregate masses of 500–1,500 kg). This seems very large relative to the home ranges of extant carnivores, but may reflect the harsh realities of life in Pleistocene Europe, where competition for prey was intense and secondary biomass was low. (Relative to African savannahs, the highest prey biomasses seen by Neandertals were likely to have been in open country during cold inter-

vals and were probably on the order of 500–1,200 kg km<sup>-2</sup>).<sup>3</sup>

Still, territories of 10,000–54,000 km<sup>2</sup> seem very large for hominins who presumably lacked domesticated animals and transportation technology such as dog sleds, boats, and animal-drawn travois. In the case of the Aquitaine basin, Geneste<sup>13</sup>

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suggested that the flint at Vaufrey accumulated as a palimpsest of occupations over a geologic period during which groups exploiting different, smaller territories were converging on the cave site; that is, the 13,000 km<sup>2</sup> indicated by flint movement represents the cumulative area, whereas any particular social group exploited a smaller territory within that area. We strongly suspect that the large lithic-based estimates for the Loire Valley<sup>16</sup> and north central Europe<sup>14</sup> also reflect cumulative

accumulations or transport of flint during social mobility (long distance visiting).

There is likely to be no simple relationship between home-range size and settlement system among hunters and gatherers, but the moderate-to-large-sized territories suggested by both estimation methods do have implications with regard to Neandertal subsistence dynamics. Return trips across a territory with even a 20–40 km radius, whether from a residential camp positioned near the center or from one positioned near the margin, were unlikely to be within day-trip distance. Average walking day trip distances among modern foragers vary by sex and group, ranging from about 6–17 km for females to 12–25 km for males,<sup>2</sup> generally at walking speeds<sup>2,63</sup> between 2.2–2.6 and 4.6 km h<sup>-1</sup>; these speeds would not have been much different for Neandertals, despite their shorter limbs.<sup>4</sup> Thus unless the Neandertals were walking much farther every day than recent foragers tend to do, logistical forays to the more distant parts of their home range likely required one or more nights spent away from the residential camp. In these smaller (20–40 km radius) home ranges, a site settlement system based on limited residential moves (a radiating mobility system<sup>42</sup>) may have sufficed to ameliorate problems of biodepletion and spatial patchiness of resources, since full exploitation of the territory could likely be accomplished by day trips or one-or-two-night excursions away from the residential camp.

At larger territory sizes (that is, the upper end of the lithic-based estimates), residential moves would have been increasingly important as a positioning strategy. In the absence of transportation technology, much of the home range of groups living in large territories would simply have been outside of reasonable striking distance from the residential base. Residential moves would have been necessary to position foragers closer to temporally limited resource patches or to limit logistical mobility while uniformly exploiting the home range, thus avoiding problems of

biodepletion. Given that the energetic cost of transport per kilogram of body mass may have been 30% greater for Neandertals than for modern humans,<sup>4</sup> and that at times they may have carried external loads equivalent to 35% of their body mass,<sup>63</sup> Neandertals undoubtedly faced energetic and burden-carrying constraints on logistical foraging radii. This may have forced a heavy reliance on camp moves (that is, a circulating<sup>42</sup> mobility strategy) as a personnel positioning strategy.<sup>3,7,64–66</sup> If this was the case, it implies a very different relationship between home-range size and site settlement dynamics than what is typically seen in recent hunter-gatherers, whose larger territories are generally associated with increasingly logistically organized (radiating mobility) subsistence systems.

The use of either lithic raw material transport or carnivore ecology models to estimate Neandertal home-range size depend on multiple assumptions that are tenuous and difficult to test. At present, it is impossible to make any definitive statements about Neandertal home-range size and how it might have varied relative to environmental circumstances. Nonetheless, we hope we have demonstrated the utility of using carnivore ecology as a lens through which to view estimates derived from lithic transport data. Much is yet to be resolved about the competitive dynamics of Neandertals and European Pleistocene carnivores, where the Neandertals may have ranked in the social dominance hierarchy of the carnivore community and how this affected their use of space and their subsistence systems. The general concordance between the smaller home ranges estimated by lithic raw material transport studies and the territory sizes estimated by the wolf model, along with the difficulties inherent in trying to exploit very large territories without transportation technology, suggests to us that Neandertal home ranges were likely to have been on the order 1,000–5,000 km<sup>2</sup>, with some variation within that range depending on ecological circumstances. Even at these moderate sizes,

these home ranges, in the absence of transportation technology, would have been consistent with settlement systems that may have relied more heavily on residential than logistical movement (circulating mobility).

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