A human-neutral large carnivore? No patterns in the body mass of gray wolves (*Canis lupus*) across a gradient of anthropization

by Jacopo Cerri[1], *Carmela Musto*[2], *Federico Mattia Stefanini*[3], *Umberto di Nicola*[4], *Nicoletta Riganelli*[4], *Maria Cristina Fontana*[5], *Arianna Rossi*[5], *Chiara Garbarino*[5], *Giuseppe Merialdi*[5], *Francesca Ciuti*[6], *Duccio Berzi*[6], *Mauro Delogu*[2], *Marco Apollonio*[7]

1. *Faculty of Mathematics, Natural Sciences and Information Technologies, University of Primorska, Glagoljaška 8, 6000 Koper, Slovenia* jacopo.cerri@famnit.upr.si
2. *Department of Veterinary Medical Sciences, University of Bologna, Bologna, Italy*
3. *Dipartimento di Scienze e Politiche Ambientali, Università degli Studi di Milano "La Statale", Milano, Italy*
4. *Gran Sasso and Monti della Laga National Park, L'Aquila. Italy*
5. *Istituto Zooprofilattico Sperimentale della Lombardia e dell'Emilia-Romagna Bruno Ubertino, Brescia, Italy*
6. *Canislupus Italia, Firenze, Italy*
7. *Department of Zoology, University of Sassari, Sassari, Italy*

Abstract

English: The gray wolf (*Canis lupus*) expanded its distribution in Europe over the last few decades. To better understand the extent to which wolves could re-occupy their historical range, nowadays including anthropized landscapes, it is important to test if and how anthropization can affect fitness-related traits in this species. We modeled how anthropization was associated with the body condition of 175 wolves that were found dead in Italy between 1999 and 2021. After having accounted for ecologically-relevant confounders, we assessed how anthropization influenced *i*) the growth of wolves in their first year of age (n = 53), *ii*) sexual dimorphism between male and female adult wolves (n = 121). Wolves in anthropized areas grow up more slowly during their first year of age. This because young wolves have slightly higher body weight at 3-5 months, possibly due to the availability of human-derived food sources, but not a higher weight later. The difference in the body weight of adult females and males slightly increases with anthropization. However, this because of an increase in the body mass of males only, possibly due to sex-specific differences in dispersal and/or to "dispersal phenotypes". Anthropization in Italy does not seem to have any clear, nor large, effect on the body mass of young and adult wolves. To the best of our knowledge, this is the first time that a similar effect is reported for a large carnivore. Our findings indicates that wolves could potentially re-occupy most of their historical range in Europe, as anthropized landscapes do not seem to constrain their body mass, an important trait related to their fitness. Wolf management could therefore be needed across vast spatial scales and in anthropized areas prone to social conflicts.

Italiano: Il lupo (*Canis lupus*) è una specie che, nel corso degli ultimi decenni, ha aumentato la propria diffusione in Europa. Per capire meglio se e quanto essa potrebbe occupare nuovamente il proprio areale di distribuzione storico, che oggi include anche paesaggi antropizzati, è importante quantificare se, e quanto, il grado di antropizzazione dell'ambiente ne condizioni alcuni tratti biologici associati alla fitness. In questo studio è stata modellata l'associazione tra l'antropizzazione e la condizione corporea di 175 lupi che sono stati rivenuti morti in Italia, tra il 1999 ed il 2021. In particolare, dopo avere condizionato le analisi ad un set di fattori confondenti potenzialmente rilevanti dal punto di vista ecologico, è stata quantificata l'influenza del grado di antropizzazione dell'ambiente: *i*) sulla crescita degli individui di lupo durante il primo anno di vita (n = 53), *ii*) sul dimorfismo sessuale tra maschi e femmine adulti (n = 121). I lupi provenienti da ambienti maggiormente antropizzati sembrano avere un accrescimento più lento durante il primo anno di vita. Questo perché essi hanno un peso corporeo leggermente più alto a 3-5 mesi di età, forse per via della maggiore disponibilità di risorse trofiche di origine umana, ma non un maggiore peso corporeo nei mesi successivi. La differenza nel peso corporeo delle femmine e dei maschi adulti sembra incrementare leggermente con il grado di antropizzazione dell'ambiente. Tuttavia, questo aumento è legato soltanto ad un aumento nel peso corporeo dei maschi, forse a causa di differenze tra maschi e femmine nei processi di dispersione e/o alla presenza di "fenotipi da dispersione". In Italia, il grado di antropizzazione dell'ambiente non sembra quindi avere nessun effetto chiaro, o importante, sul peso corporeo dei lupi. Né su quello dei

https://doi.org/10.32942/osf.io/bhnqs

giovani, durante primo anno di età, né su quello degli adulti. Per quanto ne sappiamo, questo è il primo studio che rileva l'assenza di un effetto del grado di antropizzazione dell'ambiente su di un grande carnivoro. I risultati di questo studio indicano che il lupo potrebbe potenzialmente ri-occupare la maggior parte del proprio areale di distribuzione storico in Europa. Questo in virtù del fatto che il grado di antropizzazione dell'ambiente non sembra condizionarne il peso corporeo, un importante parametro biologico fortemente associato alla fitness. In questo caso, eventuali strategie di gestione della specie andrebbero quindi implementate su grosse scale spaziali, anche in aree antropizzate, dove il rischio di conflitti sociali sul tema è maggiore.

Warning/Attenzione

English: This is a ***preprint***, not a peer-reviewed study. If you do not know what a preprint is, we encourage you to read more about this type of documents (https://en.wikipedia.org/wiki/Preprint), before evaluating and citing the study.

Italiano: Il seguente documento è un ***preprint***, non uno studio che ha superato la fase di *peer-review*. Se non sapete cosa sia un *preprint*, vi incoraggiamo a saperne di più su questo tipo di documenti (https://en.wikipedia.org/wiki/Preprint), prima di valutare la qualità dello studio e di citarlo.

---

https://doi.org/10.32942/osf.io/bhnqs

Introduction

The presence of medium and large carnivores in anthropized environments increased over the last few decades, due to urban sprawl and agricultural development in the Global South [1], and a mix of socio-ecological dynamics and legal protection in the Global North [2][3][4]. Therefore, a growing number of studies explored how well these species adapted to increased levels of human presence, to improve their conservation planning and reduce the risk of conflicts with human activities.

Anthropization was found to have three macroscopic, non-neutral, effects over medium and large carnivores. In some cases, anthropized environments are sub-optimal, compared to natural ones, due to decreased prey availability [5], the influence of human activity and artificial nightlight on foraging [6][7], persistent human disturbance [8], the impact of infrastructures on population connectivity and mortality [9][10], disease transmission and competition with domestic dogs [11] and the risk of accidental intoxication [12]. These dynamics can in turn raise metabolic stress [13], and limit reproduction and survival, thus creating source-sink dynamics with undisturbed areas [14].

On other occasions, carnivores prosper in anthropized environments, attaining higher body sizes [15][16][17] and densities [18] than those reported for environments with no human presence. Mostly because of reduced competition [19] and the exploitation of alternative food sources [20][21].

Finally, on some other cases, effects are non-linear: moderate levels of anthropization seem to be advantageous [22], or detrimental [13], compared to natural environments, but these effects reverse as anthropization increases.

The expansion of the gray wolf (*Canis lupus*) in Italy and Europe calls for further research to better forecast its future trajectory. Between early 1990s and mid 2010s wolves recolonized marginal areas in Europe, due to increased forest cover and rural abandonment [3]. However, in Italy, by having already saturated undisturbed habitat patches [23], wolves further expanded into increasingly anthropized ecosystems, recovering most of their historical range. Nowadays wolves occur in peri-urban areas and even the Po plain, one the areas in Europe with the highest human density (above 650 inhabitants/Km^2). Understanding the suitability of anthropized areas for wolves in Italy, could be pivotal to evaluate the extent to which the species could re-occupy its historical range in Europe and to forecast the spatial scale of future mitigation measures or zonation policies [24].

Considered the ecology and behavior of the gray wolf, all the three scenarios are equally plausible. In the first one, anthropized areas could be sub-optimal, as wolves could not efficiently replace large ungulates [25] and may suffer from disease transmission from domestic dogs [11]. Alternatively, anthropized areas could be favorable for wolves, which could exploit unlimited food waste [26]. Finally, wolves could show non-linear response to anthropization, as areas with intermediate level of anthropization could still offer large ungulates together with domestic animals and food waste at the same time.

This study is a first attempt to address this gap by analyzing: *i*) the temporal growth in the body weight of wolves during their first year of age and *ii*) differences in the body weight of adult male and female wolves, across a gradient of urbanized areas in central Italy, in timespan of 22 years.

Methods

Study area

The study area encompasses the Emilia-Romagna region, the northern provinces of the Tuscany region, and the Gran Sasso and Monti della Laga National Park, in the Abruzzo region, in Italy (Fig. 1).

In Emilia-Romagna and Tuscany, two contiguous regions, a wolf population of at least 97 packs was estimated between 2012 and 2016 [27]. In the 90's wolves were dived in two distinct sub-populations, one in the Apennine ridge and one in coastal and hilly part of central-southern Tuscany and Latium, which subsequently merged as the species expanded its distribution around 2013 [28]. In the Gran Sasso and Monti della Laga National Park available estimates indicate a population of 11-14 packs [29]. Both areas suffered from wolf-dog hybridization, conflicts with livestock and wolf illegal killings (Scandura et al. in prep)[27][30].

The landscape includes a variety of different ecosystems, ranging from coastal areas characterized by Mediterranean maquis to temperate broad-leaved forests and sub-alpine grasslands in the Apennines. Moreover, Emilia-Romagna and Tuscany regions host among the highest densities of wild ungulates in Europe [31], while the Abruzzo region is a hotspot for sheep farming, with more of 160,000 recorded sheep in 2020 (`https://www.vetinfo.it/j6_statistiche/#/report-pbi/89`). Urbanization is concentrated into lowlands. The portion of the study area in the Emilia-Romagna and Tuscany regions hosts a population of 8.2 million people, across 45,438 km^2 (180 inhabitants/km^2), while the

Gran Sasso and Monti della Laga park spans across 1500 km^2 with a population of 138,669 people (92.5 inhabitants/km^2).

Collection of dead wolves and laboratory analyses

The age of each animal was estimated on the basis of dental development, body size and weight [32], dividing individuals between 1-12 months, 13-24 months or older. Until 24 months, individuals were aged by assuming they were born on the 1st of May [33]. We also recorded total length (from the nose to the junction of the tail), the length of the tarsus and tail, the height of the ear, and chest and neck circumferences.

Our dataset included 107 wolves from the Emilia-Romagna and Tuscany region, as well as 68 wolves from the Abruzzo region. All these animals had been found dead and recovered by local authorities between 1999 and 2021. The proportion of males, the age of recovered wolves, the season when they were found and the number of roadkills were similar between Abruzzo and the Emilia-Romagna/Tuscany region (Supplementary Information, Appendix 1). We discarded only a single individual, which was a pup with a length of 28 cm, as it was non-informative for the purposes of the study.

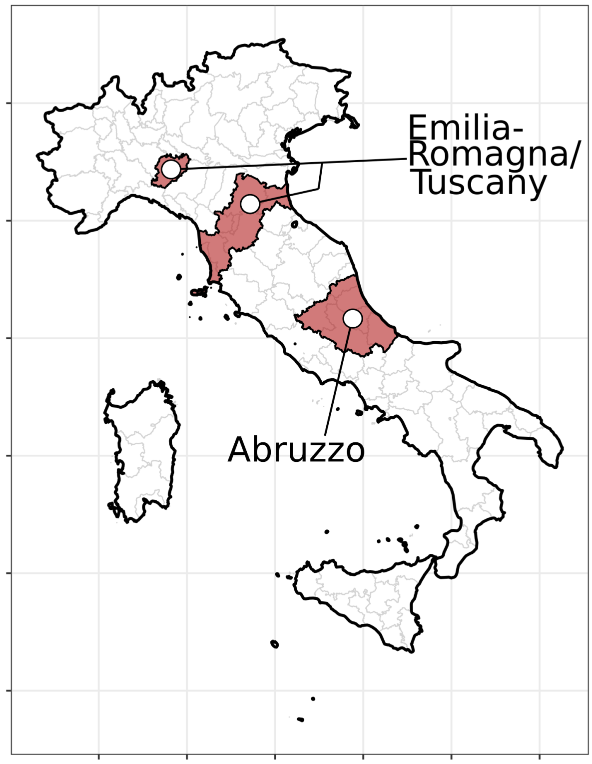

Figure 1: Map of the study area, representing provinces covered by data collection (highlighted) in Italy.

Statistical analyses and hypotheses

We modeled the effect of increased anthropization over the body mass of wolves, through two different approaches. First, we explored how anthropization influenced the growth in the body mass of wolves during their first year of age, whereas in the second step we modeled how anthropization influenced sexual dimorphism between male and female adult individuals. Thus, our relationships of interest were two interactions between anthropization and: *i*) the age in days of wolf cubs and *ii*) the sex of adult individuals.

In both cases response was the body mass of individuals. Body mass is strongly related to body condition, which, in mammals, is often measured as the ratio between body mass and total body length [34][35]. We rather modeled the contribution of body length to body mass through a linear predictor, as this approach ensured a higher level of flexibility, for example by allowing for non-linear relationships or heteroskedasticity.

In wolves, during the first year of age (n = 53), body mass increases progressively and, net the effect of total body length, it is positively associated with a better nutritional status. While during their first month wolf cubs could be fed with food waste, the role of conventional preys become progressively more important as individuals approach adulthood and hunting strategies are developed [36]. Thus, the extent to which a certain environment is optimal for cubs is measured by the strength of the temporal growth in body mass, net the effect of total body length. If the environment provides more food sources, young wolves grow up faster and the linear interaction would therefore be positive, reinforcing the effect of age in days over body mass (positive interaction). On the other hand, if environments are sub-optimal, young wolves grow up slower and the effect of age in days over body mass would be weaker (negative interaction).

For adult wolves (n = 121), with an age of two or more years, when they had completed their growth [37][38], we explored sexual dimorphism in their body mass. Sexual dimorphism in mammals can be positively associated to environmental productivity and food availability [39]. Therefore, the difference in the weight of males and females can be taken as an indicator for environmental productivity, indicating if anthropization increases or decreases available trophic resources. Namely, in case anthropization is favourable for wolves, we predicted sexual dimorphism to increase.

Body mass was measured as the weight of dead individuals that had been recovered, in kg. Urbanization was measured by means of the Human Footprint Index (hereinafter HFI), obtained by combining multiple layers about man-made structures from satellite, at the resolution of 1 km [40]. The median HFI was calculated in a buffer with a radius of 6 km around the point. This size corresponded to an area of approx. 113 km^2 around the point, reflecting the most recent estimates for the home range of the species reported in Italy [41][42].

We controlled for candidate confounding variables, through the so-called "back door criterion" [43]. A complete overview of candidate confounders, acting through some unobserved mediating variables, is shown in Fig. 2, in the form of a Directed Acyclic Graph (DAG). The sex of wolves was included because it acts both on the presence of wolves in urbanized areas and on their body mass. Wolves are dimorphic mammals and males weight more than females [44]. Moreover, available evidence also suggests that dispersal is more common for males [27][45] and as undisturbed remote areas have been firstly occupied by resident packs in Italy [23], males should be more prone to be found in urbanized environments.

We also controlled for some temporal variables that characterized sampling. The day of the year could have affected the level of urbanization of recovered wolves, because human presence in natural environments, and the probability of recovering wolf carcasses, is higher during summer or during the hunting season in autumn and early winter. In adult wolves, these seasons could also be characterized by a higher availability of preys, such as young ungulates, compared to winter and spring. Moreover, our data collection covered 22 years and thus we controlled for the year on which each wolf was found. As the wolf population steadily expanded its distribution in Italy, wolves were forced to disperse more and more in urbanized areas, while at the same time they could also have increased their average body condition due to the increased abundance of prey species, such as large ungulates. Moreover, as our data had been collected on two separate geographical blocks, corresponding to the Emilia-Romagna/Tuscany and the Abruzzo region, we controlled for this spatial heterogeneity with a dichotomous covariate.

As we found that wolves in the Emilia-Romagna/Tuscany area had a more heterogeneous total body length, we controlled for this variable also on the conditioned variance of total body mass [46].

Models were fitted through the "brms" R package [47]. The response variable was modeled as a Student's-t distribution which, for wolves of one year of age, was truncated at zero. For each parameter, we selective a moderately informative prior distribution, corresponding to a Normal distribution with mean equal to zero and a variance of one [48]. Models had 5000 MCMC iterations and a burn-in of 1000 iterations. Variables were standardized and centered, before being included in the model. Model selection was based on a backward approach, starting by the most complex model with a spline term and removing one term per time, then comparing nested models by means of leave-one-out cross validation [49].

We performed two types of sensitivity analyses. First, we tested for "collapsibility", or the extent to which our interaction terms of interest were susceptible to the removal of confounders, that were deemed redundant by leave-one-out cross. Ideally, the removal of unnecessary confounders should not have changed the posterior distribution of interaction terms that we were interested in. Then, once we identified the best candidate model, we performed a sensitivity analysis, by refitting models with the median HFI, calculated on buffers with a radius between 4 and 16 km. This practice created circles with an area between 12 and 800 km^2, which exceeded the whole spectrum of values reported for the core area and the home range of the species in Italy, which attains a maximum of approx. 400 km^2 [41].

https://doi.org/10.32942/osf.io/bhnqs

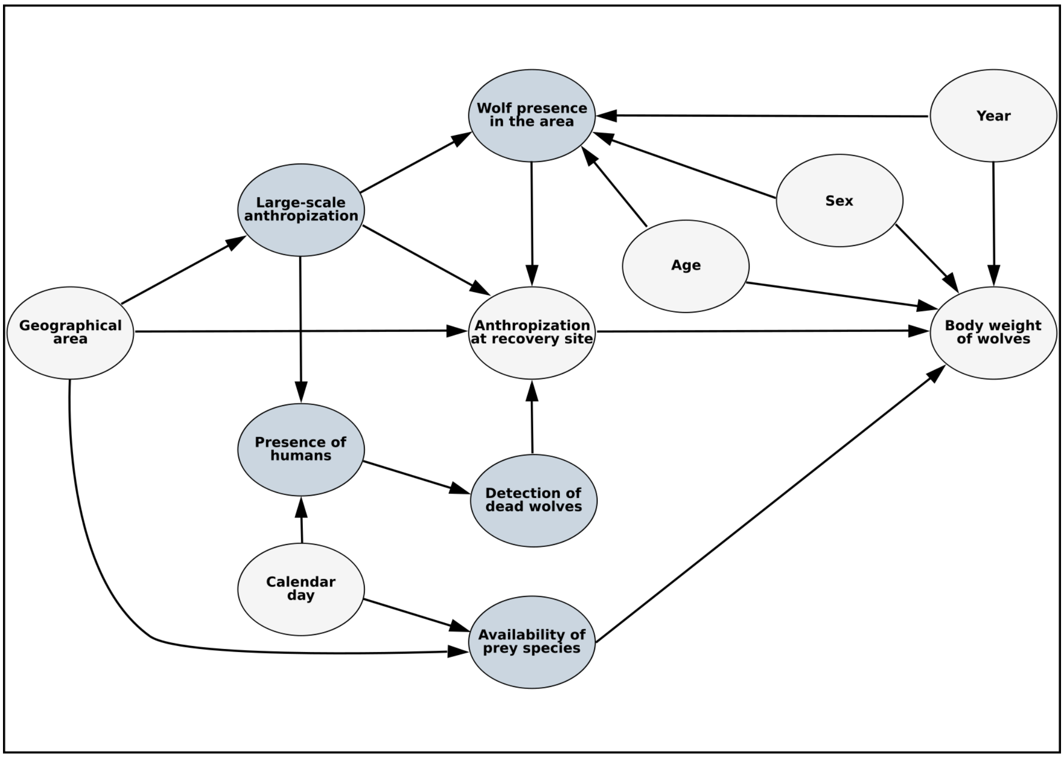

Figure 2: Directed Acyclic Graph (DAG), showing the causal relationships of interest and candidate confounders that were included in model selection (light color) and unobserved mediators (dark color). Total body length is not shown, as the predictor was included in the model not as a confounder, but to rule out the part of body mass that did not depend upon body condition, but upon differences in the size of animals.

Results

Our best candidate model predicting the growth in the body mass of wolves during their first year explained 79.0% of total variability in the response. The year when wolves were found was the only confounding variable that was retained. The body mass of young wolves increased throughout their first year of age but, net the effect of body length, the magnitude of this change was rather mild. Moreover, the growth in body mass became further milder as anthropization increased (Table 1, Fig. 3).

The best candidate model predicting differences in body mass between adult male and female wolves explained 57.8% of total variability in the response. The best candidate model retained the area where individuals had been found as a confounder, and as a predictor of variability in body mass. The body mass of male wolves showed a mild increase, for increasing levels of anthropization, but the body mass of females did not (Table 1, Fig. 4). This decreased predictive accuracy, compared to the model for wolves in their first year of age, probably depended upon the impossibility of correctly aging individuals older than three years, and thus to account for age-related variability in their body mass, which increases until 6-8 years of age [50].

The removal of redundant confounders (Table S1, Table S2) did not change the interactive effect between anthropization and the age of wolves during their first year (Fig. 5), nor the interaction between anthropization and the sexual dimorphism in weight among adult wolves (Fig. 6). Moreover, findings from best candidate models did not change, when calculating anthropization on buffers of different size (Animation S1, S2). In both models, the analyses of model residuals indicated linear relationships and the semivariogram did not highlight any residual isotropic spatial correlation (Supplementary Information, Appendix 2).

Discussion and conclusions

To the best of our knowledge, this research was among the first ones [22] assessing the impact of anthropization over the body condition of a large carnivore, the gray wolf, which is occupying increasingly anthropized landscapes in Italy and Europe. While other studies proved that the gray

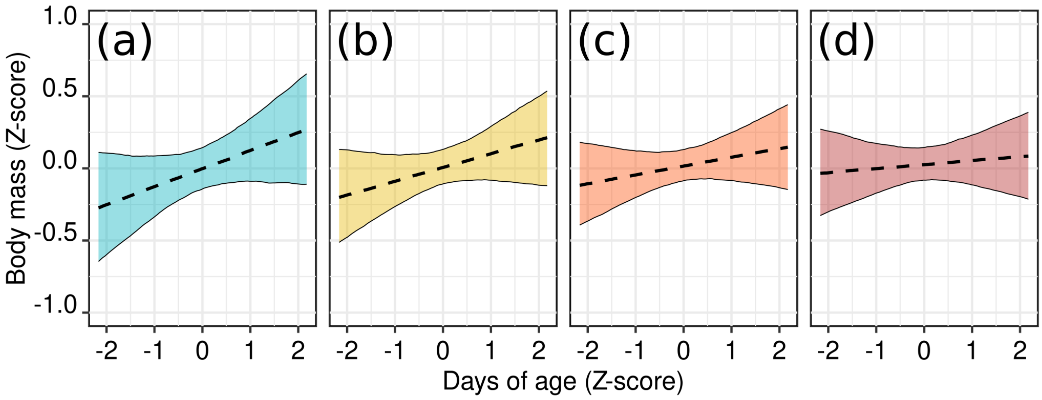

Figure 3: Interactive effect of anthropization and the age in days of recovered wolves of 1 year of age. Variables are standardized and centered. Plots correspond to the first (a), second (b), third (c) and fourth (d) quartiles of the distribution of median Human Footprint Index, calculated in a buffer with a 6-km radius around the point where animals were found. Plots (a) to (d) therefore corresponds to increasingly urbanized areas.

wolf [25][26] can exploit foods resources characterizing anthropized environments, we assessed if these environments can also affect the body condition of individuals.

This question is non-trivial, because the increased availability of alternative food sources, characterizing anthropized environments, does not automatically translate into an increased body condition of large carnivores. While food waste is abundant and rather predictable in space, thus decreasing foraging costs [51], its nutritional quality might be suboptimal, as it includes a high proportion of carbohydrates which are not processed by the grey wolf which, compared to the domestic dog, is devoid of alpha-amylase [52] and with a different composition of gut microbiotas [53]. Moreover, foraging in urban environments can be influenced by human disturbance, which raises stress [54], and energetic costs [55].

Our findings provide preliminary evidence that wolves, at least in Italy, are capable to cope with anthropized landscapes in a way which is different from what has been reported for other large carnivores: anthropized landscapes seem not to have any clear effect on the body mass of individuals. Or, most likely, anthropized landscapes do not show any clear tradeoff between negative and positive effects.

The body mass of young wolves in our sample grew throughout their first year of age, net the effect of an increase in total body length. This reflected an increase in their muscular mass and fat, two components of body condition. However, this growth had only a very mild interaction with anthropization (Fig. 2). More anthropized areas had young wolves which grew up in a less pronounced way during their first year, but which have higher body masses at 3-5 months of age, suggesting a positive influences on the weight of human derived food sources in the first months of life, i.e. when pup rising is entirely dependent from adults provisioning. This pattern does not provide any clear evidence on whether anthropized environments are optimal or suboptimal for young wolves in their first year of life as a whole. Perhaps, anthropized environments can provide an abundance of food resources which could be exploited by young wolves during their first weeks, but less preys such as large ungulates which may be better to sustain individuals at 10-12 months. These differences could also be explained with a different size of wolf packs. Anecdotical evidence indicates that anthropized environments in Italy might have smaller packs often represented by a pair with pups. This may be favorable in areas with fewer large preys [56] and a rich disposal of small food items represented by garbage and pets but might not pay out well in most of our study area, characterized by high densities of ungulates [31].

The effect of anthropization over sexual dimorphism in adult wolves is also partially unclear. While we found a moderate increase of this character, as areas became more anthropized, its magnitude was relatively low (Fig. 3). Most interestingly, an increase in weight involved only male wolves whether females did not increase in body mass at all. Even if in large mammals it was shown that food shortage/abundance may constrain/favor the growth of males and females differentially [57], the lack of female weight increase under potential favorable condition opens another explanation related to sex-specific differences in the dispersal behavior of wolves, which is more common for males [27] and the consequent presence of "dispersal phenotypes" in our sample. In mammals, individuals who disperse usually have a larger size [58]. Considered the progressive saturation of undisturbed, remote habitats (Zanni et al. submitted), dispersing individuals, which are often large males, mostly moved to more anthropized areas, thus entering our sample.

https://doi.org/10.32942/osf.io/bhnqs

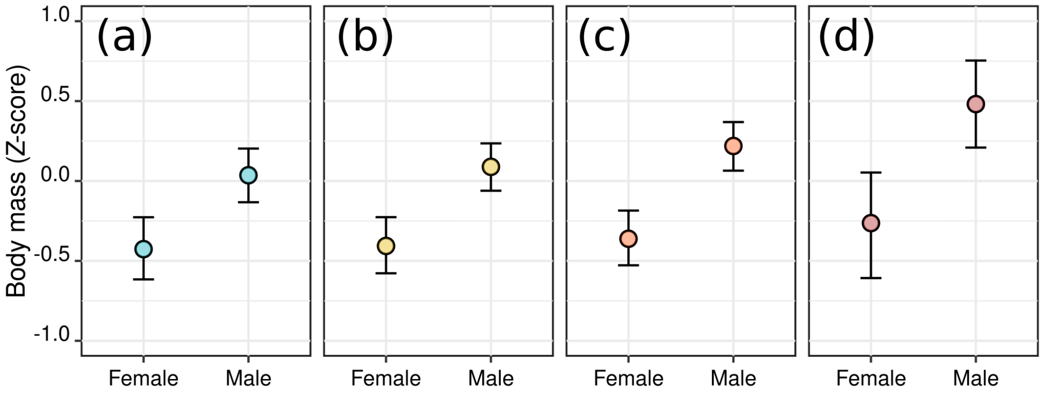

Figure 4: Interaction between anthropization and the sex of recovered adult wolves. Variables are standardized and centered. Plots correspond to the first (a), second (b), third (c) and fourth (d) quartiles of the distribution of median Human Footprint Index, calculated in a buffer with a 6-km radius around the point where animals were found. Plots (a) to (d) therefore corresponds to increasingly urbanized areas

Assessing the effect of anthropization on the body mass of wolves is also an urgent question. Body condition is strongly associated to reproduction and survival in mammals, two demographic parameters that are paramount for the long-term viability of populations. Considered the rapid expansion of the gray wolf in Europe, if anthropized environments do not have any effect on the body mass of individuals, as suggested by our study, this could mean that in the near future wolves could colonize, reproduce and survive in a significant portion of their historical range in Europe. Thus, policies for co-existing with them, such as zonation or mitigation measures [24], will be needed across vast spatial scales and their implementation might generate a widespread social debate, as it might go beyond rural areas [59].

Considered the potential impacts of a widespread wolf presence in anthropized landscapes of Europe, our findings urgently call for replication studies, addressing two main points. First, studies should replicate our analyses in other geographical areas. Wild ungulates are core preys for wolves and our study covers some of the areas in Europe with the highest densities of ungulates, whose populations increased over the last two decades and which became widespread even in urbanized settings. Other European countries faced a decrease in the wild boar, a key prey, due to the African Swine Fever [60], have high numbers of unprotected livestock and different presence of waste in the environment. Thus, in these areas, the impact of anthropization over the body mass of wolves can be different.

At the same time, we also emphasize the need for studies based on much larger samples. While we found no significant effect of urbanization on the growth and sexual dimorphism of wolves, considered our sample size we cannot rule out that an effect with a low magnitude actually exists: statistical power increases with sample size and nuanced interactions can be reliably quantified only by analyzing thousands of observations. In this study we did not perform power analysis, because we had no prior knowledge about effect size and because we aimed to provide only preliminary evidence. However, if other studies will adopt similar sample sizes, there will be no significant advancement in terms of statistical power and it will be impossible to capture small environmental effects, which could nevertheless be potentially important in the long term. As our findings raise serious questions about the potential expansion of wolves in Europe, research group should pool together their data through collaborative platforms to address them.

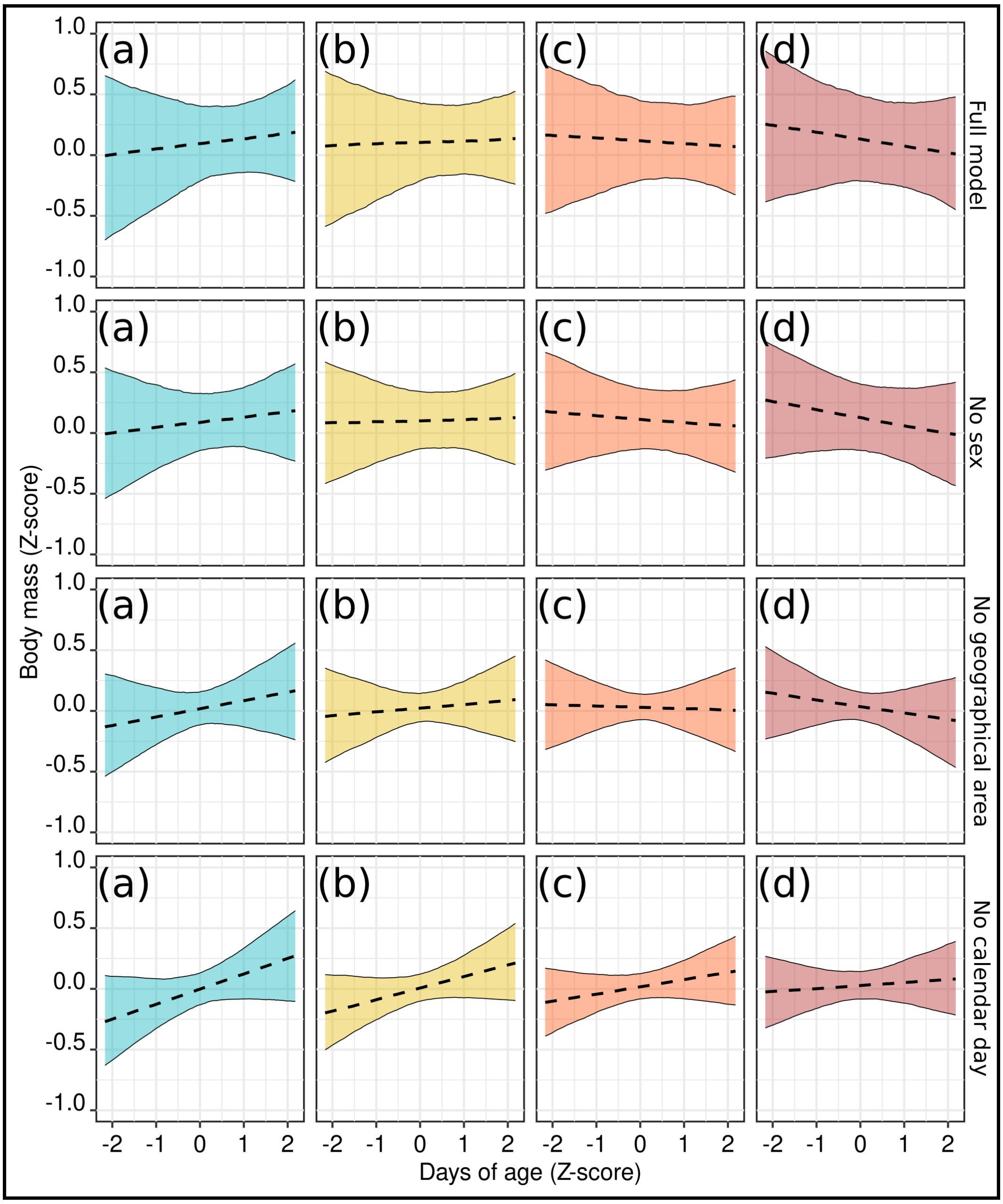

Figure 5: Effect of the removal of redundant confounders, over the interaction between anthropization and the age in days of recovered wolves of 1 year of age. Plots correspond to the first (a), second (b), third (c) and fourth (d) quartiles of the distribution of median Human Footprint Index, calculated in a buffer with a 6-km radius around the point where animals were found. Plots (a) to (d) therefore corresponds to increasingly urbanized areas.

https://doi.org/10.32942/osf.io/bhnqs

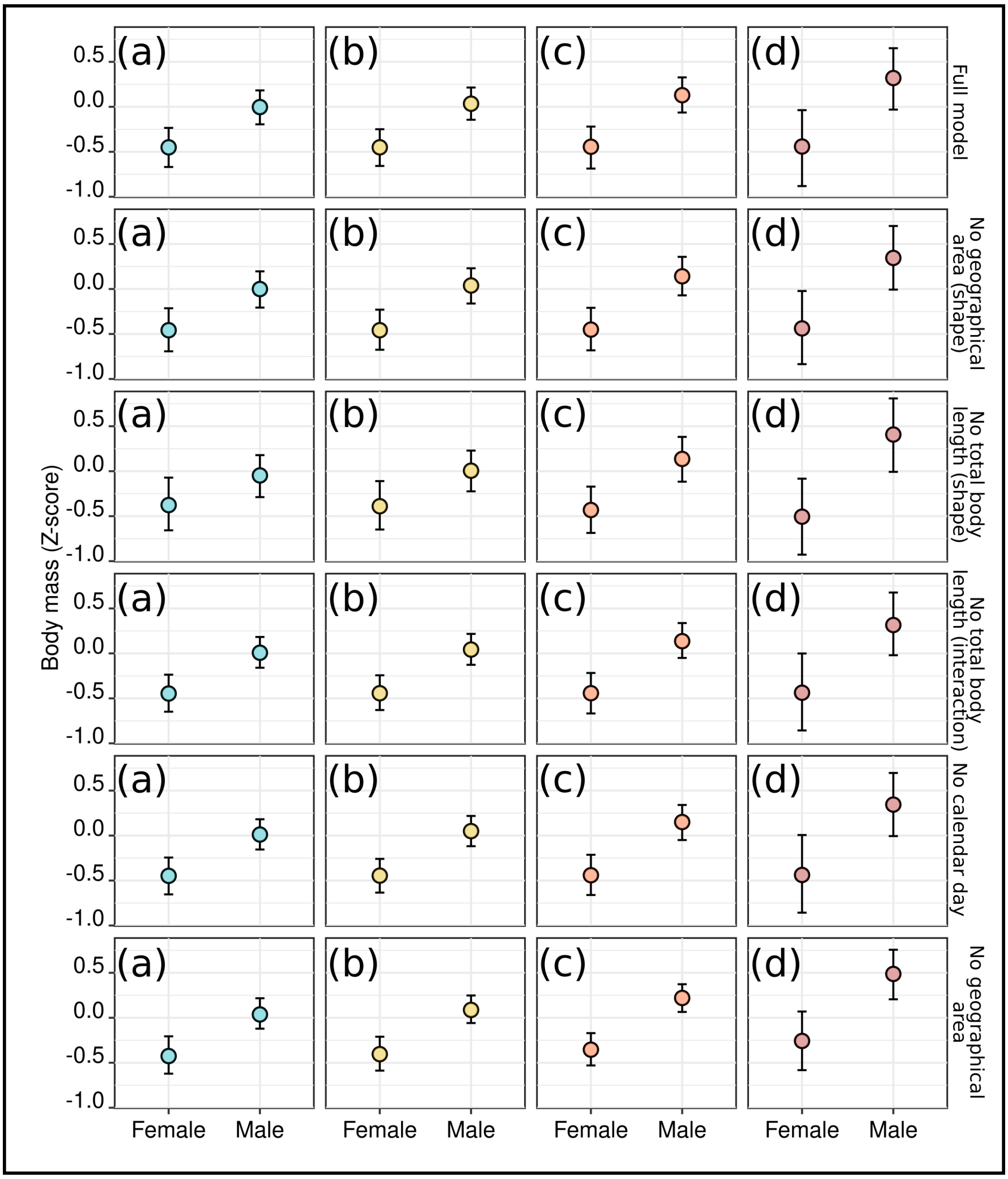

Figure 6: Effect of the removal of redundant confounders, over the interaction between anthropization and the weight dimorphism of adult wolves. Plots correspond to the first (a), second (b), third (c) and fourth (d) quartiles of the distribution of median Human Footprint Index, calculated in a buffer with a 6-km radius around the point where animals were found. Plots (a) to (d) therefore corresponds to increasingly urbanized areas.

Body mass in wolves of 1 year of age			
	Estimate	**S.E.**	**95% Credibility Interval**
Intercept	0.03	0.05	(-0.07)/(0.14)
Age in days	0.06	0.06	(-0.06)/(0.18))
Anthropization	0.03	0.06	(-0.08)/(0.13))
Year when animals were found	-0.12	0.06	(-0.23)/(-0.01))
Total body length	0.75	0.07	(0.61)/(0.88))
Age in days : Anthropization	-0.09	0.06	(-0.20)/(-0.03))
Body mass in adult wolves			
	Estimate	**S.E.**	**95% Credibility Interval**
Intercept	-0.36	0.09	(-0.53)/(-0.19)
Sex (Male vs Female)	0.58	0.12	(0.36)/(0.80)
Anthropization	0.08	0.10	(-0.13)/(0.28)
Total body length	0.59	0.06	(0.48)/(0.71)
Sex : Anthropization	0.15	0.13	(-0.12)/(0.40)

Table 1 Outputs of the best candidate model for body mass of wolves in their first year of age, and for adult wolves. Anthropization is calculated on a buffer with a 6km radius around the points where animals had been found.

References

1. Di Minin, E., *et al*. (2016). Global priorities for national carnivore conservation under land use change. *Scientific reports*, 6(1), 1-9. https://doi.org/10.1038/srep23814
2. Chapron, G., *et al*. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346(6216), 1517-1519. https://doi.org/10.1126/science.1257553
3. Cimatti, M., *et al*. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*. https://doi.org/10.1111/ddi.13219
4. Miller, S. D., *et al*. (2013). Conservation and management of large carnivores in North America. *International journal of environmental studies*, 70(3), 383-398 https://doi.org/10.1080/00207233.2013.801628
5. Wolf, C., & Ripple, W. J. (2016). Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science*, 3(8), 160252 https://doi.org/10.1098/rsos.160252
6. Ditmer, M. A., *et al*. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore. *Ecography*, 44(2), 149-161. https://doi.org/10.1111/ecog.05251
7. Wilmers, C. C., *et al*. (2021). COVID-19 suppression of human mobility releases mountain lions from a landscape of fear. *Current Biology*, 31(17), 3952-3955. https://doi.org/10.1016/j.cub.2021.06.050
8. Ripari, L., *et al*. (2022). Human disturbance is the most limiting factor driving habitat selection of a large carnivore throughout Continental Europe. *Biological Conservation*, 266, 109446. https://doi.org/10.1016/j.biocon.2021.109446
9. Kozakiewicz, C. P., *et al*. (2019). Urbanization reduces genetic connectivity in bobcats (*Lynx rufus*) at both intra–and interpopulation spatial scales. *Molecular Ecology*, 28(23), 5068-5085. https://doi.org/10.1111/mec.15274
10. Morales-González, *et al*. (2020). Large carnivores living alongside humans: Brown bears in human-modified landscapes. *Global Ecology and Conservation*, 22, e00937. https://doi.org/10.1016/j.gecco.2020.e00937
11. Millán, J., *et al*. (2016). Patterns of exposure of Iberian wolves (*Canis lupus*) to canine viruses in human-dominated landscapes. *Ecohealth*, 13(1), 123-134 https://doi.org/10.1007/s10393-015-1074-8
12. Serieys, L. E., *et al*. (2018). Urbanization and anticoagulant poisons promote immune dysfunction in bobcats. *Proceedings of the Royal Society B: Biological Sciences*, 285(1871), 20172533. https://doi.org/10.1098/rspb.2017.2533
13. Carroll, R. P., *et al*. (2021). Bobcat Hair Cortisol Correlates with Land Use and Climate. *The Journal of Wildlife Management*, 85(4), 772-781. https://doi.org/10.1002/jwmg.22029
14. Lamb, C. T., *et al*. (2020). The ecology of human–carnivore coexistence. *Proceedings of the National Academy of Sciences*, 117(30), 17876-17883. https://doi.org/10.1073/pnas.1922097117
15. Hantak, M. M., *et al*. (2021). Mammalian body size is determined by interactions between climate, urbanization, and ecological traits. *Communications biology*, 4(1), 1-10. https://doi.org/10.1038/s42003-021-02505-3
16. Yom-Tov, Y. (2003). Body sizes of carnivores commensal with humans have increased over the past 50 years. *Functional Ecology*, 323-327. https://www.jstor.org/stable/3599086

17. Lunn, N. J. & Stirling, I. (1985). The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. *Canadian Journal of Zoology*, 63, 2291–2297. https://cdnsciencepub.com/doi/10.1139/z85-340
18. Green, D. S., *et al.* (2019). Can hyena behaviour provide information on population trends of sympatric carnivores?. *Philosophical Transactions of the Royal Society B*, 374(1781), 20180052. https://doi.org/10.1098/rstb.2018.0052
19. Green, D. S., *et al.* (2018). Anthropogenic disturbance induces opposing population trends in spotted hyenas and African lions. *Biodiversity and Conservation*, 27(4), 871-889. https://doi.org/10.1007/s10531-017-1469-7
20. Abay, G. Y., *et al.* (2011). Peri-urban spotted hyena (Crocuta crocuta) in Northern Ethiopia: diet, economic impact, and abundance. *European Journal of Wildlife Research*, 57(4), 759-765. https://doi.org/10.1007/s10344-010-0484-8
21. Newsome, T. M., *et al.* (2015). The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*, 24(1), 1-11. https://doi.org/10.1111/geb.12236
22. Coon, C. A., *et al.* (2019). Effects of land-use change and prey abundance on the body condition of an obligate carnivore at the wildland-urban interface. *Landscape and urban planning*, 192, 103648. https://doi.org/10.1016/j.landurbplan.2019.103648
23. Bassi, E., *et al.* (2015). Predicting the spatial distribution of wolf (*Canis lupus*) breeding areas in a mountainous region of Central Italy. *PloS one*, 10(6), e0124698 https://doi.org/10.1371/journal.pone.0124698
24. Mech, L. D. (2017). Where can wolves live and how can we live with them?. *Biological conservation*, 210, 310-317. https://doi.org/10.1016/j.biocon.2017.04.029
25. Zlatanova, D., *et al.* (2014). Adaptive diet strategy of the wolf (Canis lupus L.) in Europe: a review. *Acta zoologica bulgarica*, 66(4), 439-452. https://acta-zoologica-bulgarica.eu/downloads/acta-zoologica-bulgarica/2014/66-4-439-452.pdf
26. Newsome, T. M., *et al.* (2016). Food habits of the world's grey wolves. *Mammal Review*, 46(4), 255-269. https://doi.org/10.1111/mam.12067
27. Caniglia, R., *et al.* (2014). Noninvasive sampling and genetic variability, pack structure, and dynamics in an expanding wolf population. *Journal of Mammalogy*, 95(1), 41-59. https://doi.org/10.1644/13-MAMM-A-039
28. Apollonio, M., *et al.* (2016). Esperienze di monitoraggio e conservazione del lupo in Toscana (2013-2016). https://www.isprambiente.gov.it/files2018/eventi/verso-piano-monitoraggio-lupo/APOLLONIOROMADICEMBRE2018DEFINITIVA.pdf
29. Ricci, S., *et al.* (2014). Il monitoraggio della presenza del lupo nel Parco Nazionale del Gran Sasso e Monti della Laga. IX Congresso Italiano di Teriologia, Civitella Alfedena (AQ), 7-10 Maggio 2014. https://www.researchgate.net/publication/318112744_Il_monitoraggio_della_presenza_del_lupo_nel_Parco_Nazionale_del_Gran_Sasso_e_Monti_della_Laga
30. Musto, C., *et al.* (2021). Men and wolves: are anthropogenic causes the main driver of wolf mortality in human-dominated landscapes in Italy?. *Global Ecology and Conservation*, 32, e01892. https://doi.org/10.1016/j.gecco.2021.e01892
31. Apollonio, M., *et al.* (Eds.). (2010). European ungulates and their management in the 21st century. Cambridge University Press. https://doi.org/10.1017/CBO9780511974137.002
32. Mörner, T., *et al.* (2005). Diseases and mortality in free-ranging brown bear (*Ursus arctos*), gray wolf (*Canis lupus*), and wolverine (*Gulo gulo*) in Sweden. *Journal of Wildlife Diseases*, 41(2), 298-303. https://doi.org/10.7589/0090-3558-41.2.298
33. Boitani, L. (1981). Lupo *Canis lupus*. In: Pavan, M. (Eds.), Distribuzione e biologia di 22 specie di Mammiferi in Italia (pp. 61–67). Rome. https://www.ibs.it/distribuzionebiologia-di-22-specie-libri-vintage-vari/e/2560038844628
34. Labocha, M. K., *et al.* (2014). Which body condition index is best?. *Oikos*, 123(1), 111-119. https://doi.org/10.1111/j.1600-0706.2013.00755.x
35. Lovari, S., *et al.* (2007). Mortality parameters of the wolf in Italy: does the wolf keep himself from the door?. *Journal of Zoology*, 272(2), 117-124. https://doi.org/10.1111/j.1469-7998.2006.00260.x
36. Imbert, C., *et al.* (2016). Why do wolves eat livestock?: Factors influencing wolf diet in northern Italy. *Biological Conservation*, 195, 156-168. https://doi.org/10.1016/j.biocon.2016.01.003
37. Mech, L. D. (2006). Age-related body mass and reproductive measurements of gray wolves in Minnesota. *Journal of Mammalogy*, 87(1), 80-84. https://doi.org/10.1644/05-MAMM-F-212R1.1
38. Stahler, D. R., *et al.* (2013). The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. *Journal of Animal Ecology*, 82(1), 222-234. https://doi.org/10.1111/j.1365-2656.2012.02039.x
39. Isaac, J. L. (2005). Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, 35(1), 101-115. https://doi.org/10.1111/j.1365-2907.2005.00045.x
40. Venter, O., *et al.* (2016). Global terrestrial Human Footprint maps for 1993 and 2009. *Scientific data*, 3(1), 1-10. https://doi.org/10.1038/sdata.2016.67
41. Mancinelli, S., *et al.*(2018). Determinants of home range size and space use patterns in a protected wolf (*Canis lupus*) population in the central Apennines, Italy. *Canadian Journal of Zoology*, 96(8), 828-838. https://doi.org/10.1139/cjz-2017-0210

42. Mattioli, L., *et al*. (2018). Estimation of pack density in grey wolf (*Canis lupus*) by applying spatially explicit capture-recapture models to camera trap data supported by genetic monitoring. *Frontiers in zoology*, 15(1), 1-15. https://doi.org/10.1186/s12983-018-0281-x

43. Elwert, F. (2013). Graphical causal models. In Handbook of causal analysis for social research (pp. 245-273). Springer, Dordrecht. https://doi.org/10.1007/978-94-007-6094-3

44. Boitani, L., *et al*. (2003). Fauna d'Italia. Mammalia III. Carnivora-Artiodactyla. https://www.researchgate.net/publication/281837570_Fauna_d%27Italia_mammalia_III_Carnivora-Artiodactyla

45. Ausband, D. E. (2022). Inherit the kingdom or storm the castle? Breeding strategies in a social carnivore. *Ethology*, 128(2), 152-158. https://doi.org/10.1111/eth.13250

46. Umlauf, N., & Kneib, T. (2018). A primer on Bayesian distributional regression. *Statistical Modelling*, 18(3-4), 219-247. https://doi.org/10.1177%2F1471082X18759140

47. Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software*, 80, 1-28. https://doi.org/10.18637/jss.v080.i01

48. Lemoine, N. P. (2019). Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos*, 128(7), 912-928. https://doi.org/10.1111/oik.05985

49. Vehtari, A., *et al*. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and computing*, 27(5), 1413-1432. https://doi.org/10.1007/s11222-016-9696-4

50. Hilderbrand, G. V., & Golden, H. N. (2013). Body composition of free-ranging wolves (*Canis lupus*). *Canadian journal of zoology*, 91(1), 1-6. https://doi.org/10.1139/cjz-2012-0205

51. Petroelje, T. R., *et al*. (2019). Subsidies from anthropogenic resources alter diet, activity, and ranging behavior of an apex predator (*Canis lupus*). *Scientific reports*, 9(1), 1-9. https://doi.org/10.1038/s41598-019-49879-3

52. Axelsson, E., *et al*. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, 495(7441), 360-364. https://doi.org/10.1038/nature11837

53. Lyu, T., *et al*. (2018). Changes in feeding habits promoted the differentiation of the composition and function of gut microbiotas between domestic dogs (*Canis lupus familiaris*) and gray wolves (*Canis lupus*). *Amb Express*, 8(1), 1-12. https://doi.org/10.1186/s13568-018-0652-x

54. Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: a question of evolving, acclimatizing or coping with urban environmental stress. *Functional Ecology*, 29(7), 913-923. https://doi.org/10.1111/1365-2435.12477

55. Nickel, B. A., *et al*. (2021). Energetics and fear of humans constrain the spatial ecology of pumas. *Proceedings of the National Academy of Sciences*, 118(5). https://doi.org/10.1073/pnas.2004592118

56. Zimmermann, B., *et al*. (2015). Predator-dependent functional response in wolves: From food limitation to surplus killing. *Journal of Animal Ecology*, 84(1), 102-112. https://doi.org/10.1111/1365-2656.12280

57. LeBlanc, M., *et al*. (2001). Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology*, 79(9), 1661-1670. https://doi.org/10.1139/z01-128

58. Ims, R.A. & Hjermann, D.Ø. (2001) Condition-dependent dispersal. Dispersal (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 203–216. Oxford University Press, Oxford. https://global.oup.com/academic/product/dispersal-9780198506591?cc=us&lang=en&

59. Manfredo, M. J., *et al*. (2020). The changing sociocultural context of wildlife conservation. *Conservation Biology*, 34(6), 1549-1559. https://doi.org/10.1111/cobi.13493

60. Morelle, K., *et al*. (2020). Disease-induced mortality outweighs hunting in causing wild boar population crash after african swine fever outbreak. *Frontiers in veterinary science*, 378. https://doi.org/10.3389/fvets.2020.00378

Acknowledgments

We thank the Provincial Police, the Local Health Authority (ASL) and the Forest Police of each province included in this study. We also thank the "Wild Animal Recovery Center" and the Canislupus Italia Association for providing assistance in the recovery of wolf carcasses. CM and MA were partially supported by a research grant funded by the Vienna Science and Technology Fund (Project number: WWTF ESR20-009).

Author's contribution

JC, CM and MA conceived the ideas and designed methodology; CM, UdN, NR, MCF, AR, CG, GM, FC, DB, MD and MA managed and provided the data; JC and FMS analysed the data; JC, CM, FMS and MA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Dataset and reproducible software code

The dataset, altogether with the reproducible software code and animations (Animation S1 and S2) are available on the Open Science Framework repository, at the following link: https://osf.io/g2jsv/

Supplementary Information

Appendix 1 - Comparison of recovered wolves between Emilia-Romagna/Tuscany and Abruzzo regions

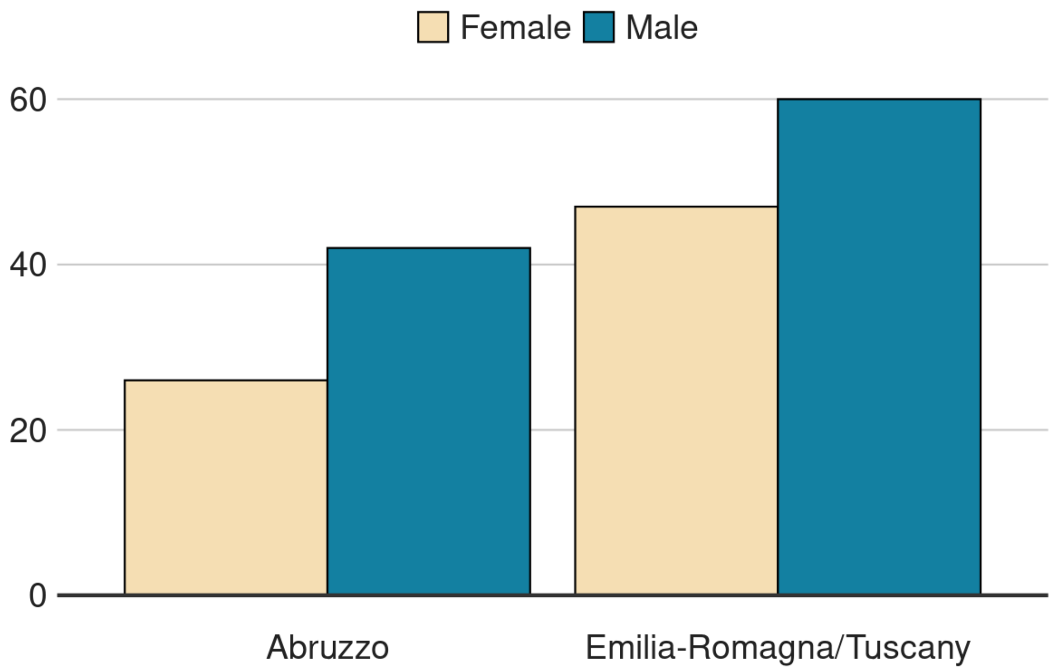

Figure S1: Number of female and male wolves, between Abruzzo and Emilia-Romagna/Tuscany region. The number of recovered wolves is shown on the y-axis.

https://doi.org/10.32942/osf.io/bhnqs

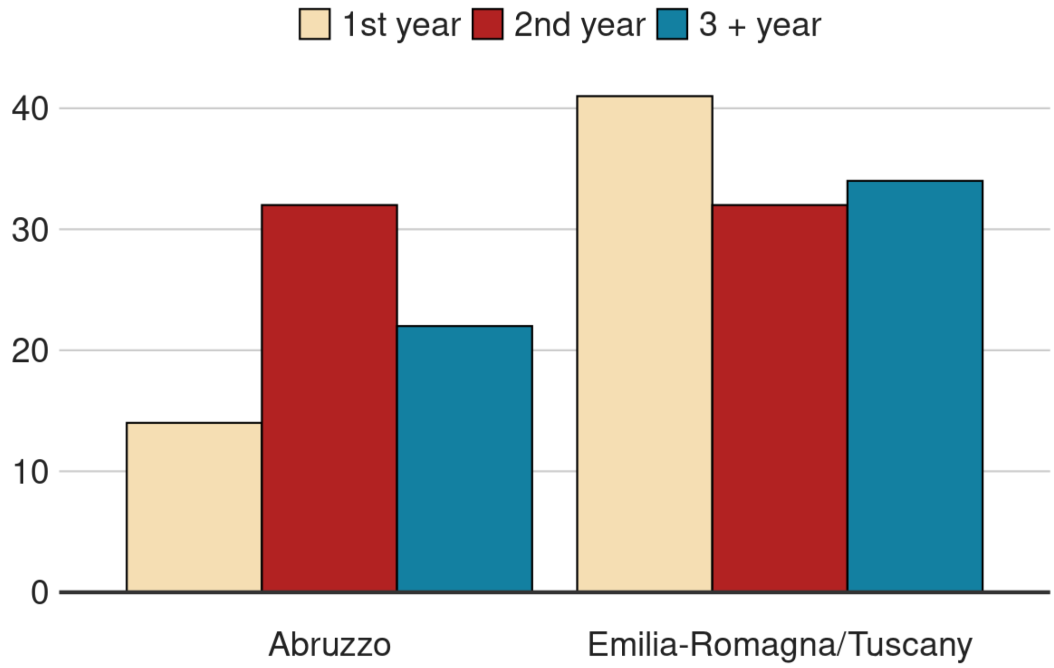

Figure S2: Distribution of wolves of different age classes, between Abruzzo and Emilia-Romagna/Tuscany region. The number of recovered wolves is shown on the y-axis.

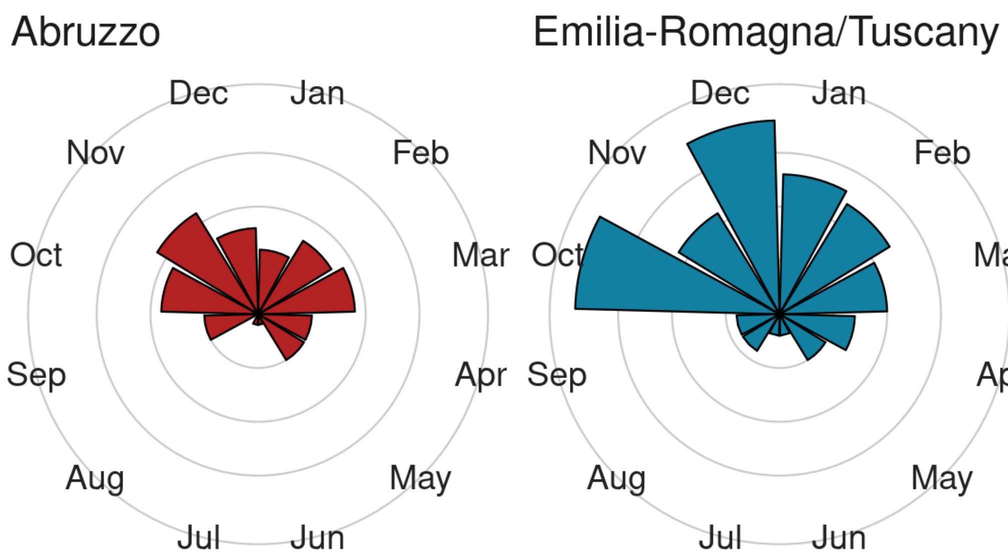

Figure S3: Distribution of recovered wolves, between Abruzzo and Emilia-Romagna/Tuscany region, across the different months of the year.

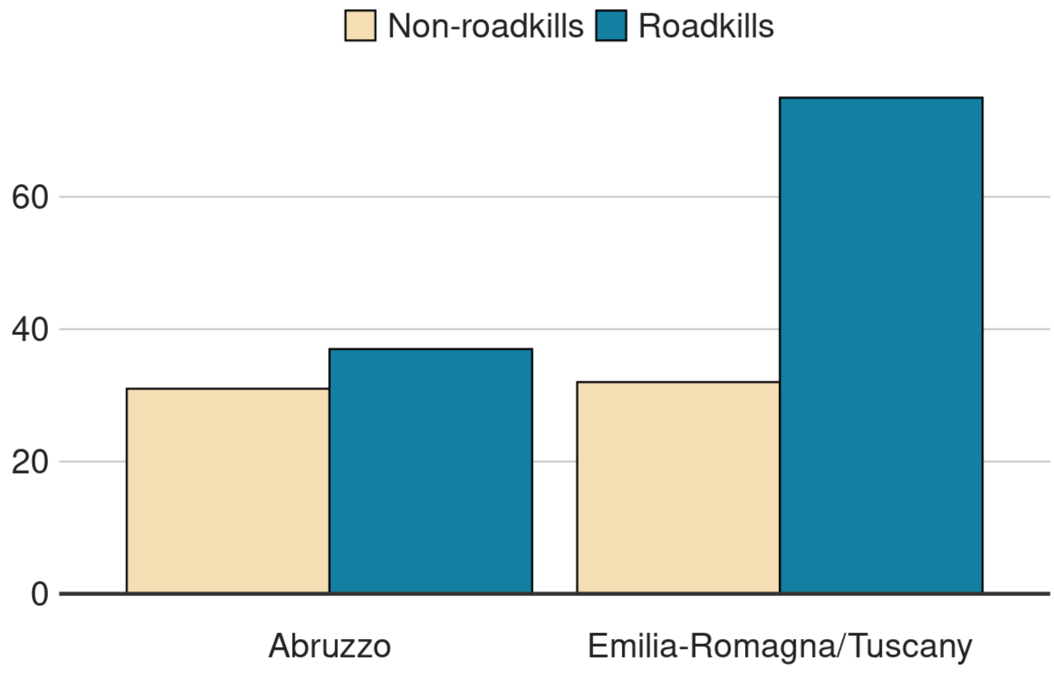

Figure S4: Distribution of recovered wolves that had been involved in collisions with vehicles, between Abruzzo and Emilia-Romagna/Tuscany region. The number of recovered wolves is shown on the y-axis.

Appendix 2 - Model selection: removal of redundant confounders

Model formula	ELPD ± S.E.
Body mass ~anthropization + age in days + day of the year when animals were found + year when animals were found + area + sex + age in days : anthropization + total body length	-33.1 ± 7.5
Body mass ~anthropization + age in days + day of the year when animals were found + year when animals were found + area + age in days : anthropization + total body length	-32.0 ± 7.6
Body mass ~anthropization + age in days + day of the year when animals were found + year when animals were found + age in days : anthropization + total body length	-31.2 ± 7.4
Body mass ~anthropization + age in days + year when animals were found + age in days : anthropization + total body length	-30.4 ± 8.1
Body mass ~anthropization + age in days + age in days : anthropization + total body length	-30.5 ± 8.4

Table S1 Theoretical expected log-pointwise predictive density (ELPD) and its standard error (S.E.), obtained from leave one-out cross-validation. Outputs from models about the body mass of wolves in their first year of age (left).

Model formula	ELPD ± S.E.
Conditional mean: Body mass ~anthropization + day of the year when animals were found + year when animals were found + area + sex + sex : anthropization + total body length Conditional variance: total body length + area	-120.9 ± 8.9
Conditional mean: Body mass ~anthropization + day of the year when animals were found + year when animals were found + area + sex + sex : anthropization + total body length Conditional variance: total body length	-122.9 ± 9.6
Conditional mean: Body mass ~anthropization + day of the year when animals were found + year when animals were found + area + sex + sex : anthropization + total body length	-122.9 ± 9.6
Conditional mean: Body mass ~anthropization + day of the year when animals were found + area + sex + sex : anthropization + total body length Conditional variance: total body length + area	-119.9 ± 8.5
Conditional mean: Body mass ~anthropization + sex + sex : anthropization + total body length Conditional variance: total body length + area	-119.9 ± 8.6

Table S2. Theoretical expected log-pointwise predictive density (ELPD) and its standard error (S.E.) from leave one-out cross-validation. Outputs from models about adult wolves..

https://doi.org/10.32942/osf.io/bhnqs

Appendix 3 - Overview of model residuals and semivariogram from the best candidate models

Wolves of first year of age (see Table 1 for model outputs)

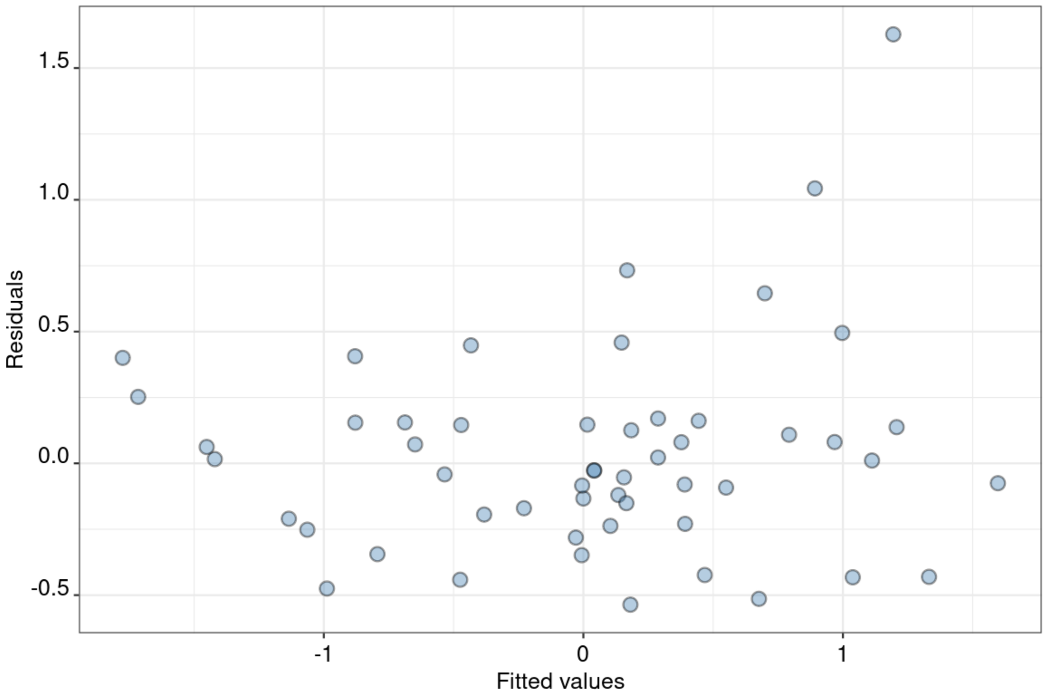

Figure S5: Residuals versus fitted values from the best candidate model.

https://doi.org/10.32942/osf.io/bhnqs

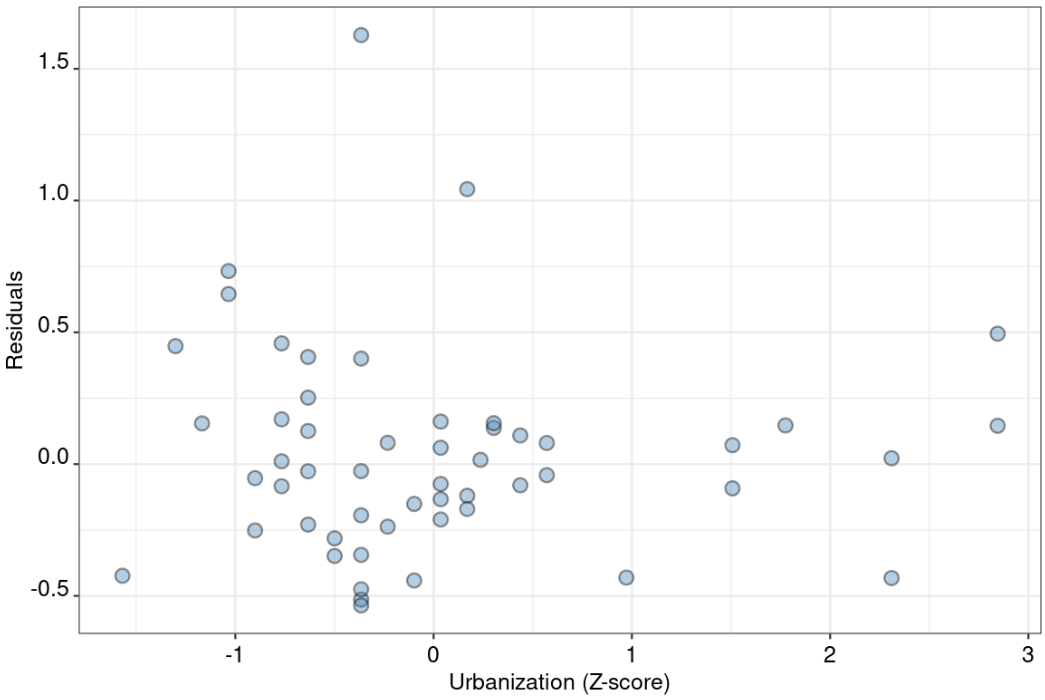

Figure S6: Residuals from the best candidate model versus standardized and centered scores of the Human Footprint Index.

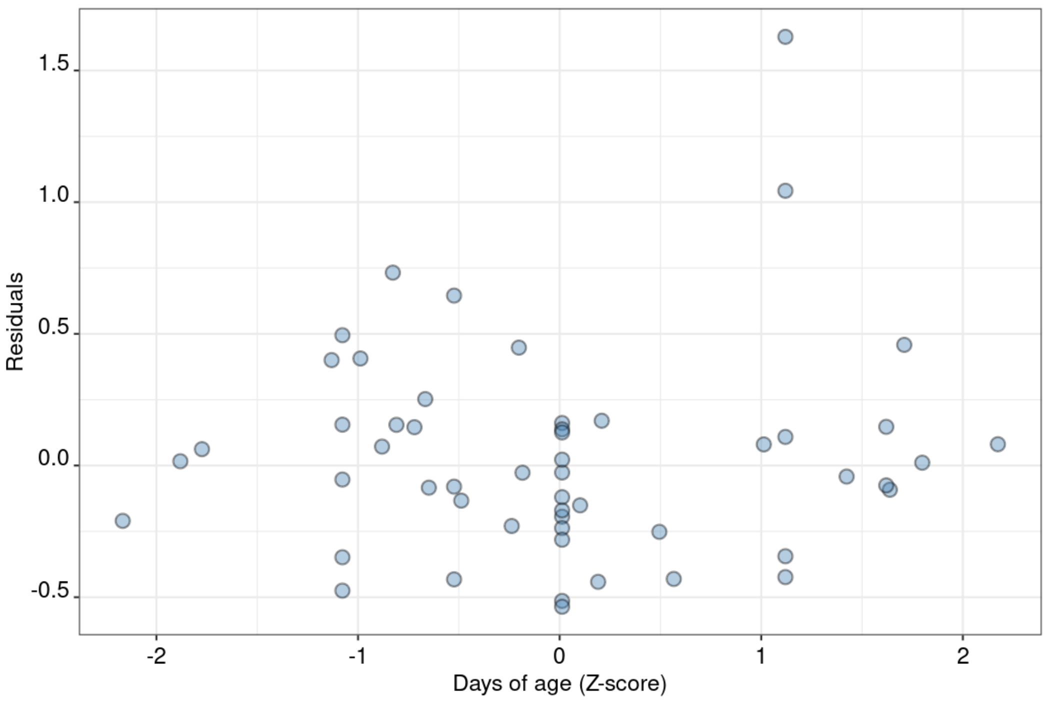

Figure S7: Residuals from the best candidate model versus standardized and centered scores of the age in days of recovered wolves.

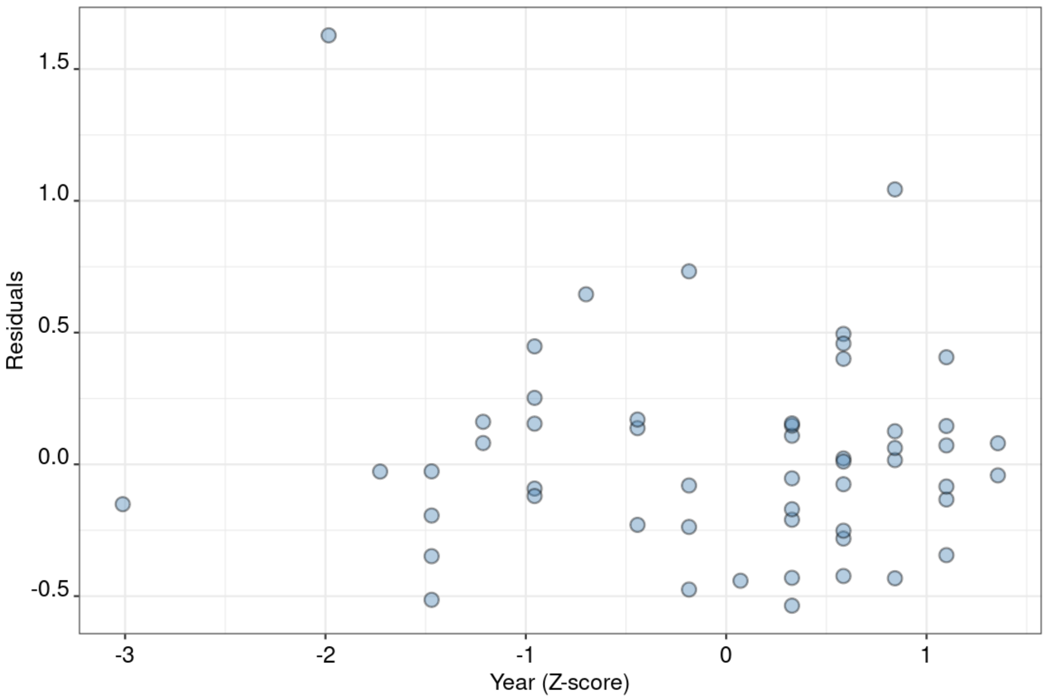

Figure S8: Residuals from the best candidate model versus standardized and centered scores of the year when wolves were recovered.

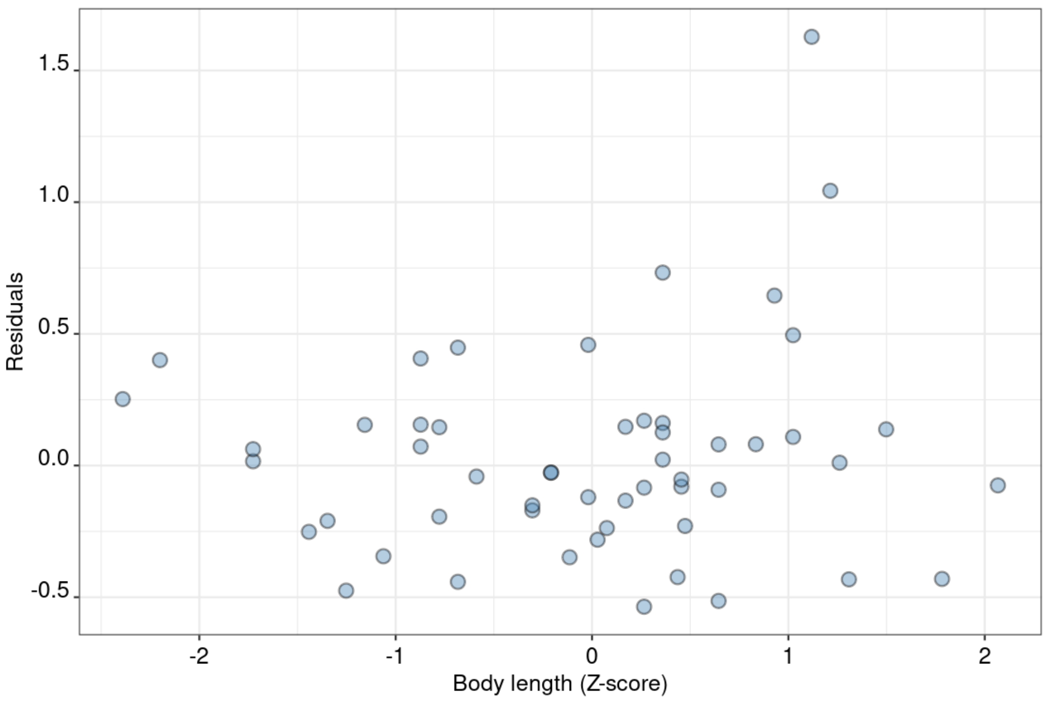

Figure S9: Residuals from the best candidate model versus standardized and centered scores of the total body length.

https://doi.org/10.32942/osf.io/bhnqs

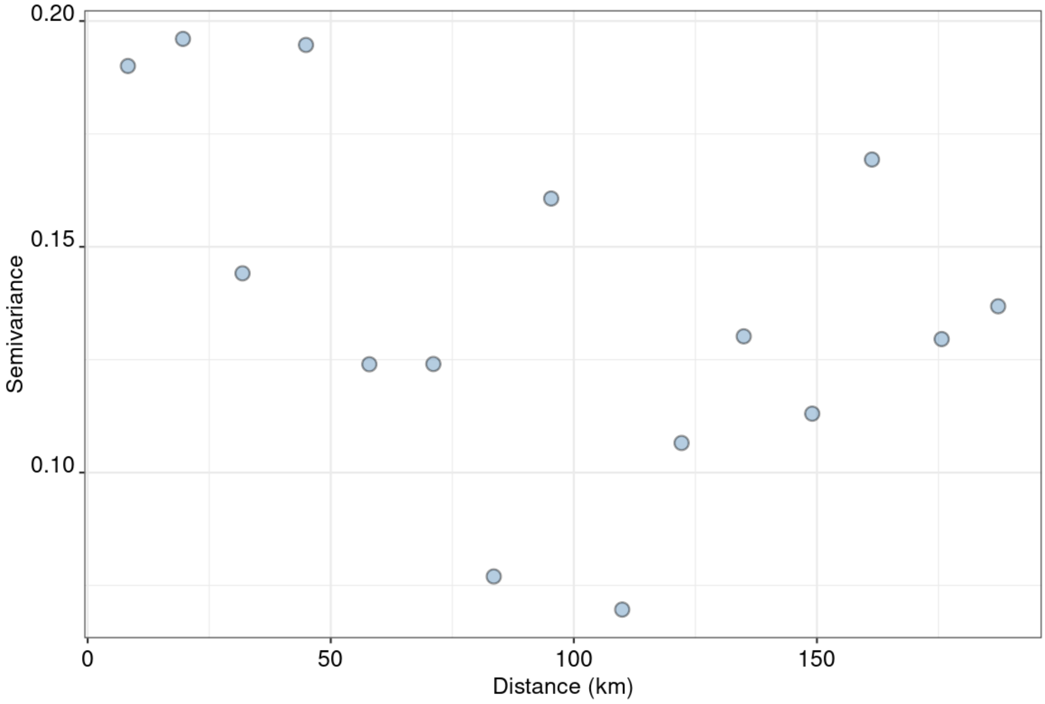

Figure S10: Isotropic semivariogram: semivariance of model observations in function of distance between sites where wolves were recovered.

Wolves of two or more years (see Table 1 for model outputs)

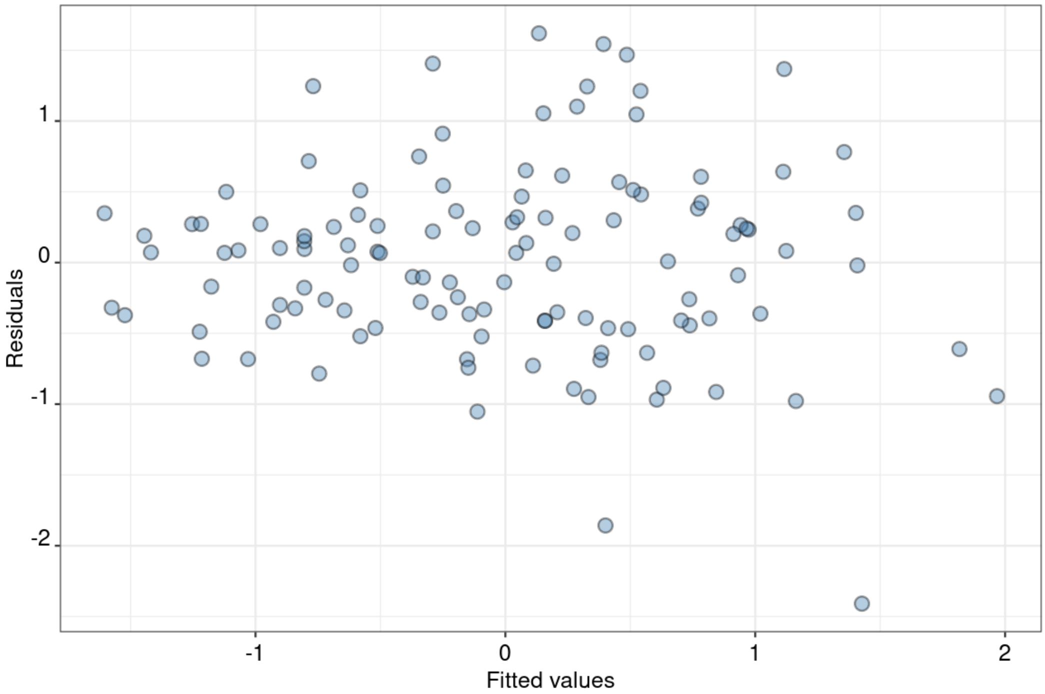

Figure S11: Residuals versus fitted values from the best candidate model.

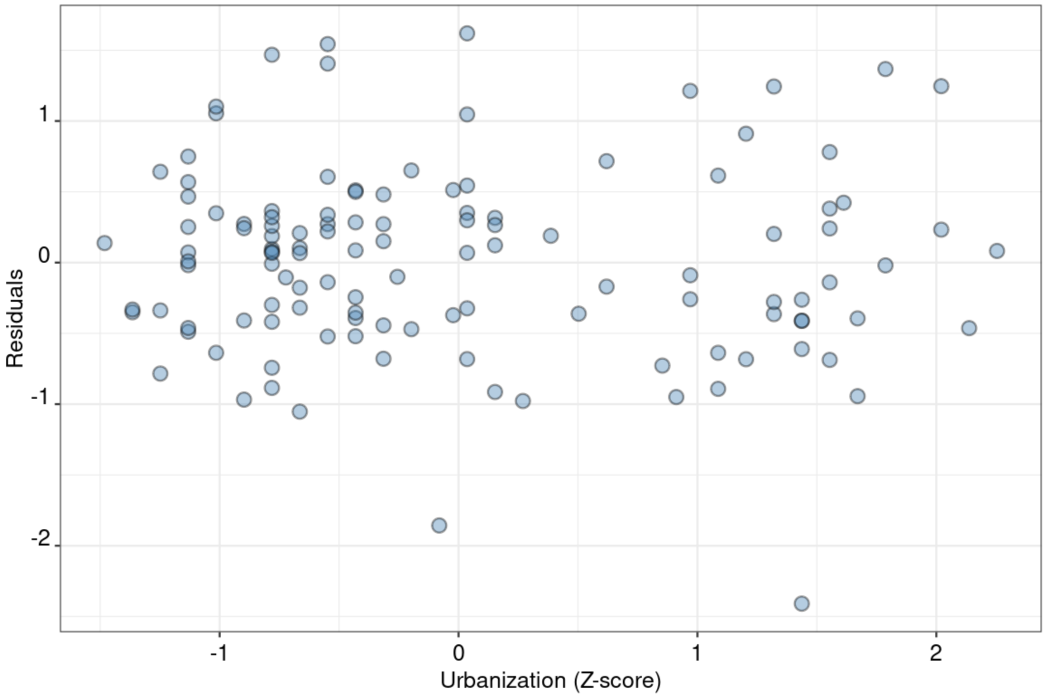

Figure S12: Residuals from the best candidate model versus standardized and centered scores of the Human Footprint Index.

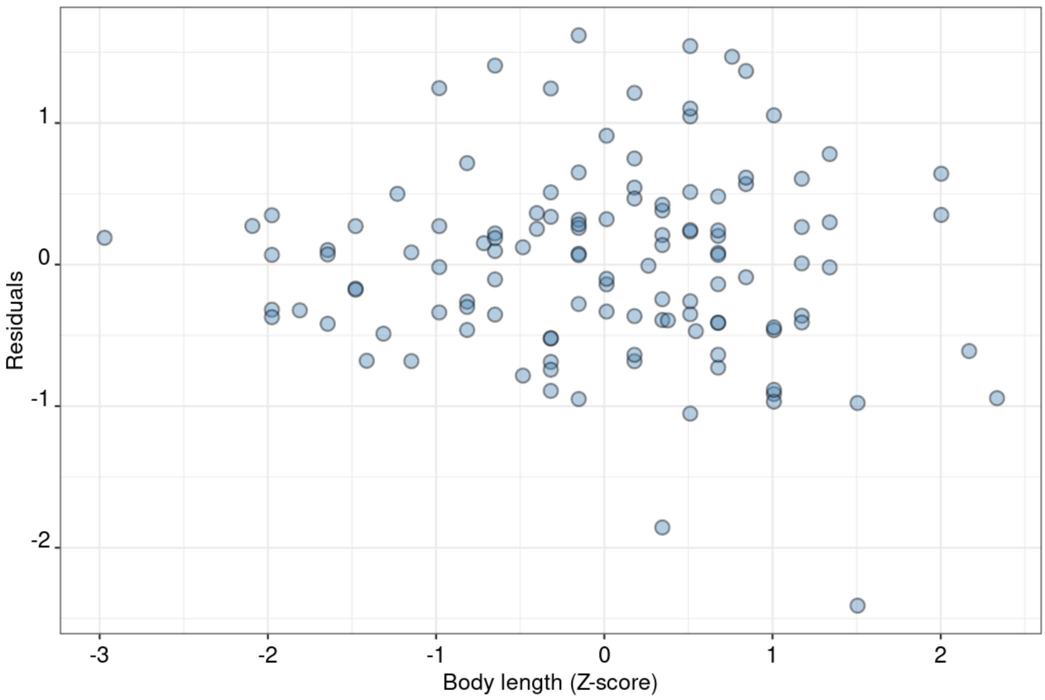

Figure S13: Residuals from the best candidate model versus standardized and centered scores of the total body length.

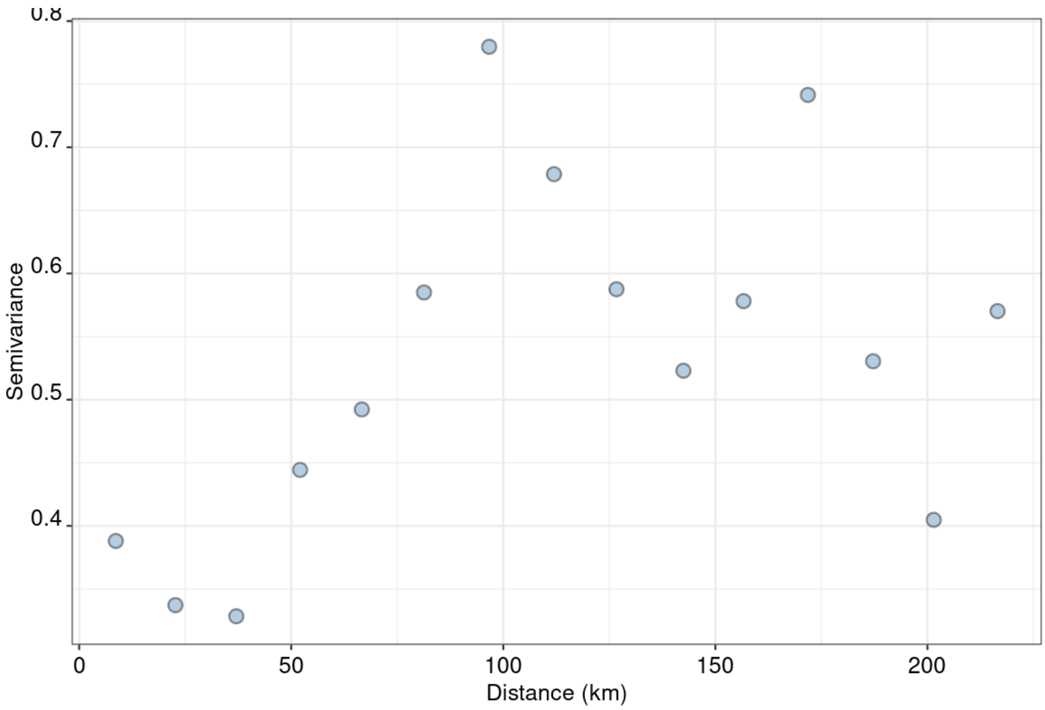

Figure S14: Isotropic semivariogram: semivariance of model observations in function of distance between sites where wolves were recovered.

https://doi.org/10.32942/osf.io/bhnqs