

Making a New Dog?

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We are in the middle of a period of rapid and substantial environmental change. One impact of this upheaval is increasing contact between humans and other animals, including wildlife that take advantage of anthropogenic foods. As a result of increased interaction, the evolution and function of many species may be altered through time via processes including domestication and hybridization, potentially leading to speciation events. We discuss the ecological and management importance of such possibilities, using gray wolves and other large carnivores as case studies. We identify five main ways that carnivores might be affected: changes to social structures, behavior and movement patterns, changes in survivorship across wild- to human-dominated environments, evolutionary divergence, and potential speciation. As the human population continues to grow and urban areas expand while some large carnivore species reoccupy parts of their former distributions, there will be important implications for human welfare and conservation policy.

Keywords: Anthropocene, carnivore, domestication, hybridization, speciation

Artificial selection and domestication have been integral to the success of humankind, who have been exploiting the genetic diversity of plants and animals for over 12,000 years (Driscoll et al. 2009). Success, however, has come at a cost: As a consequence of human-driven environmental change (the Anthropocene), the Earth is now experiencing massive biodiversity loss, with extinction rates estimated to be 1000 times higher than background levels (Pimm et al. 2014). Under this new world order, many species are being forced to adapt to new conditions and to coexist closely with humans. This process can be viewed as a form of domestication, because domestication itself concerns adaptations to a captive environment (Price 1984). Developing an in-depth understanding of how human-induced alterations of the environment might shape the evolution of species—and, in turn, of their effects on ecosystem functioning—is therefore integral to our ability to conserve and manage the natural world.

Although it is difficult to generalize about the effects of human alterations of landscapes on all species, it is possible to draw lessons by focusing on particular groups of species that have similar ecological roles and functions. Large carnivores provide an obvious starting point because they are widely distributed, they are known to have strong effects on ecosystems, and many of them live in close proximity to humans (Chapron et al. 2014, Ripple et al. 2014). Also, large carnivores include gray wolves (*Canis lupus*), which have had a long and complex relationship with humans, being the first domesticated animal. Indeed, the processes by which wolves were originally domesticated provide an ideal case study from which to learn because there are several corollary processes that continue to take place today.

In particular, although there is debate about the precise timing and location of gray-wolf domestication (to domestic dogs, *Canis familiaris*; Larson et al. 2012), the mechanism by which wolves were domesticated is generally agreed to have been via their increasing reliance on anthropogenic foods (Zelder 2012). Specifically, recent evidence suggests that the early ancestors of modern dogs thrived on a diet rich in starch relative to the carnivorous diet of wolves (Axelsson et al. 2013). By implication, the attraction of free-ranging wolves to food waste around human encampments was likely the key first step in the domestication process, which was then catalyzed by the rising availability of anthropogenic subsidies that accompanied the development of sedentary human communities associated with the agricultural revolution. Furthermore, differences in synaptic plasticity between wolves and domestic dogs suggest that learning promoted the enhanced use of human resources and wolf-human interaction (Li et al. 2014). Therefore, the early phase of wolf domestication was more likely the result of an ecological niche shift characterized by increasing *commensalism* (one species benefits from another without affecting it) rather than a process directed by humans (Zelder 2012).

The process of gray-wolf domestication is important to highlight because large quantities of human-provided foods are intentionally or unintentionally provided by humans to animal communities all around the world (Oro et al. 2013). Access to these “anthropogenic foods” has the capacity to change a variety of animal life traits, including genetics, reproduction, abundance, survival, spatial distributions, and intra- and interspecific interactions (Newsome et al. 2015). But despite the likelihood that these changes will

affect ecosystem health, there is seldom recognition that the provision of anthropogenic foods is a global conservation issue and, perhaps more speculatively, the possible starting point for the domestication of wild species. Using gray wolves as a case study, we review how anthropogenic-food availability may affect these issues and, in addition, draw lessons from other carnivore species globally to highlight how humans may shape their ecology and behavior. We conclude that reliance on anthropogenic resources by contemporary gray wolves, as well as other large carnivores, may once again be initiating a commensal domestication process, and we discuss the implications of this hypothesis for the ecology, evolution, and conservation of wolves and other large carnivores, as well as for ecosystems and humans more broadly.

The story of the gray wolf

Gray-wolf populations are now thought to be globally stable, but this canid has been extirpated from large portions of its former range primarily owing to human persecution (Chapron et al. 2014, Ripple et al. 2014). Therefore, conservation efforts have focused on repatriating the wolf to previously occupied regions (e.g., the Greater Yellowstone Ecosystem in the United States). These reintroduction efforts, coupled with subsequent dispersal and relaxation of persecution, have created a scenario in which wolves are now recolonizing numerous areas. This trend had led to a groundswell of research demonstrating the ecological impacts of wolf recovery (Ripple et al. 2014).

Studies from different ecosystems suggest that as top predators, gray wolves can induce top-down forcing that reduces prey abundance (Creel et al. 2007), modifies patterns of foraging by herbivores (Kuijper et al. 2013), and suppresses smaller carnivores (Elmhagen and Rushton 2007). These top-down effects can flow through communities via multiple pathways, including modifying interactions between smaller carnivores (Newsome and Ripple 2015); affecting plant communities (Painter et al. 2014); indirectly affecting associated mammals (e.g., beavers, *Castor canadensis*; Smith and Tyers 2008) and songbirds (Baril 2009); releasing small-mammal populations (Miller BJ et al. 2012); and subsidizing scavengers (Wilmers et al. 2003). These effects, among others, have ensconced wolves as a symbol of the wilderness and have been a driving force behind efforts to maintain and restore the ecosystem services they can provide.

But although the return of gray wolves is considered a conservation success story in some places, wolves are often returning to human-modified environments, especially in Europe (Chapron et al. 2014, Dorresteijn et al. 2015). Little is known about the ecological role of wolves in such environments (Kuijper et al. 2016), but a recent review shows that wolves in settled areas often feed on anthropogenic foods such as livestock, livestock carcasses, and garbage (Newsome et al. 2016). In central Iran, for instance, gray wolves feed

almost exclusively on farmed chickens, domestic goats, and garbage (Tourani et al. 2014). In central Greece, domestic pigs, goats, and sheep dominate the gray-wolf diet (Migli et al. 2005), whereas in Western Galicia (Spain), free-ranging mountain ponies and livestock are the main prey of gray wolves (Lopez-Bao et al. 2013). These are not isolated cases; rather, anthropogenic foods occurred in 66% of the dietary studies undertaken on gray wolves since 1940, and on average, they constituted 32% of gray wolf diet around the world (Newsome et al. 2016).

The high use of anthropogenic foods by gray wolves highlights that this species continues to be attracted to these foods or is forced to eat them if wild prey is depleted. In Belarus, for example, increased consumption of livestock by gray wolves coincided with periods when wild ungulate densities were low (Sidorovich et al. 2003). A similar pattern emerges in southern Europe, where livestock consumption by gray wolves historically has been higher during periods when wild ungulates were scarce (Newsome et al. 2016), and this holds true at a global level (figure 1).

Under more natural circumstances, gray wolves are known to switch to alternate prey when their primary wild ungulate prey declines. Such prey includes beavers, lagomorphs, microtine rodents, birds, fish, and, on occasion, other carnivores (Newsome et al. 2016). However, a case study in Iran highlights that gray wolves may still consume high quantities of anthropogenic foods even when wild prey are abundant (Hosseini-Zavarei et al. 2013). This tendency reflects the opportunistic nature of wolves and their underlying attraction to foods that can be readily obtained and eaten with low energetic cost or risk of harm. Given that wolves consistently and sometimes heavily rely on anthropogenic foods, it is surprising that relatively little attention has been paid to this aspect of their foraging ecology or to its potential consequences.

The underlying issue with anthropogenic-food availability

Although the exact reasons for gray wolves using anthropogenic foods are not clear, there is emerging recognition that this practice can dramatically alter their ecology and behavior (Newsome et al. 2016). It is likely that the availability of anthropogenic foods could alter the ecological relationships of wolves, both intraspecifically (e.g., sociality, pack size, breeding rates, dispersal, and density) and interspecifically (e.g., wild predator-prey relationships, hunting behavior, trophic interactions, and bottom-up and top-down processes; Dorresteijn et al. 2015). Thus, where anthropogenic foods are abundant, the ecological effects of wolves will likely differ from those in systems with low or no human presence or effects (figure 2).

In support of this hypothesis, a recent review revealed that at least 36 species of terrestrial predator more than 1 kilogram in body size use anthropogenic foods in 34 countries worldwide (Newsome et al. 2015). In the presence of these resources, there are documented effects on predator

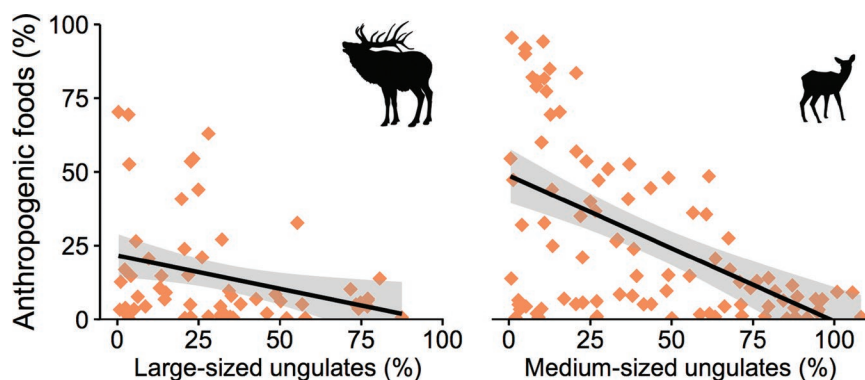


Figure 1. General linear model with a Gaussian error assessing the relationships between gray wolf (*Canis lupus*) consumption of large- (240- to 650-kilogram) and medium-sized (23- to 130-kilogram) ungulates and anthropogenic foods (livestock and garbage). Data are from Newsome and colleagues (2016); both relationships are significant ($p < .05$). Silhouettes are adapted images courtesy of the Integration and Application Network, University of Maryland.

abundance, dietary preferences, life-history parameters, and movements, as well as negative effects on co-occurring species that become more susceptible to predation (Newsome et al. 2015). To further elaborate on this emerging issue, we highlight several case studies below demonstrating that anthropogenic food availability can modify intra- and interspecific interactions involving predators, and we discuss how these changes could heighten the potential for conflict with humans. These case studies also illustrate the diverse ways that predators adapt to human-modified environments, including being driven to eat anthropogenic foods.

Dingoes, foxes, and bears. Independent studies on Australian dingoes (*Canis dingo*; Crowther et al. 2015) and free-roaming domestic dogs (*C. familiaris*), red foxes (*Vulpes vulpes*), and bears (*Ursus arctos* or *U. americanus*) demonstrate the typical responses that predators can have to increased anthropogenic food availability. In the case of dingoes, access to food scraps at a waste facility resulted in decreased home-range areas and movements, larger group sizes, and altered dietary preferences to the extent that they filled a similar dietary niche to domestic dogs (Newsome et al. 2014). Moreover, the population of subsidized dingoes was a genetically distinct cluster, possibly because of founder effects (Newsome et al. 2013). Similar responses have been documented for red foxes in Israel: In the presence of anthropogenic foods, foxes had smaller home ranges and much higher mean survival rates than in the absence of these foods (Bino et al. 2010). Genetic drift and genetic differentiation have also been found between rural and urban red fox populations in Zurich (Switzerland), because of the urban population being founded by a small number of individuals (Wandeler et al. 2003).

Bears also frequently take advantage of anthropogenic foods, and access to these foods influences bear reproductive

success, dietary preferences, and several life-history traits (Newsome et al. 2015). Interestingly, though, higher age-specific mortality of black bears has been documented in urban areas, where they forage on garbage, in comparison with wildland populations because of elevated human-caused mortalities (Beckmann and Lackey 2008). Therefore, an increase in anthropogenic food supply may not always result in gains in predator fitness, especially if there is a high probability of conflict with humans (akin to an ecological trap).

The Asiatic lion. In the Greater Gir Landscape of Western India, the last remaining population of Asiatic lions (*Panthera leo persica*) has increased over the last five decades in response to a series of conservation measures

(Banerjee et al. 2013). Although ostensibly a conservation success story, this development has been accompanied by an increase in livestock depredation in areas surrounding the Gir Protected Area (GPA), with depredation hotspots falling along the movement paths of dispersing lions (Meena et al. 2014). By implication, the continued recovery of the Gir lion population is likely to spur increased dispersal as individuals seek space outside the crowded GPA, and this could exacerbate the potential for livestock depredation (Banerjee et al. 2013). At the same time, intensive use of livestock as prey and frequent contact with humans has apparently led to a level of habituation that enables tourists to make close observations of Asiatic lions without the protection of a vehicle (Packer 2013). This kind of close contact centered on the use of anthropogenic foods can certainly drive ecotourism. However, it is also reminiscent of the process by which wolves putatively embarked on the path to domestication and, if pervasive, could at least modify the ecological relationships of lions in the Greater Gir ecosystem. Furthermore, such contact has the potential to promote negative interactions between lions and humans, which might ultimately jeopardize lion conservation.

Polar bears. Human impacts on ecosystems continue to expand through the conversion of land to agriculture and for suburban and urban development. As this encroachment continues, it is well acknowledged that more species will use anthropogenic foods where available (Oro et al. 2013, Newsome et al. 2015). However, less well known is that climate change could exacerbate this phenomenon and even force species to use anthropogenic foods. For example, in some parts of their range, polar bears (*Ursus maritimus*) are spending more time on land as an apparent response to the loss of sea ice that has accompanied climate warming

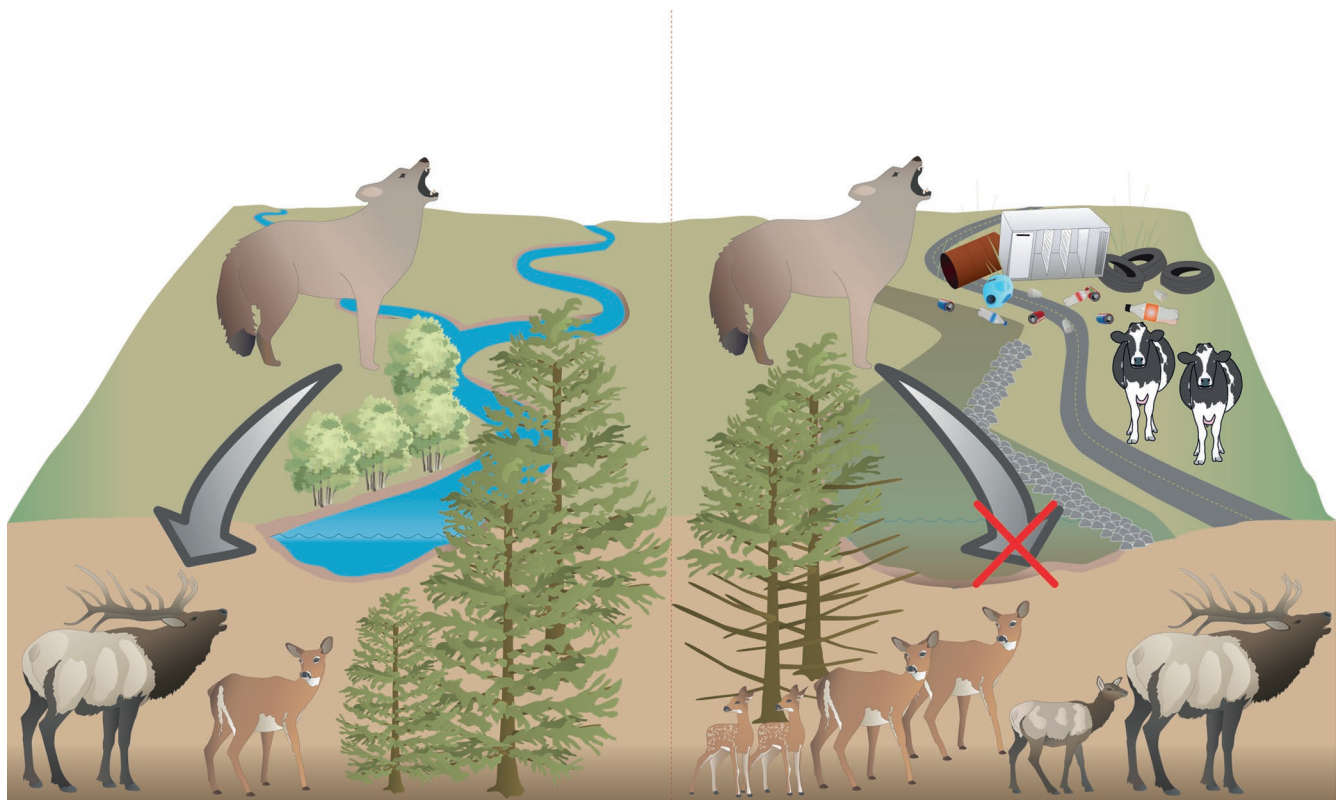


Figure 2. A hypothetical comparison of gray wolf (*Canis lupus*) ecological effects in wilderness areas (left) and human-modified systems (right) where there are abundant anthropogenic foods. For example, if gray wolves focus on eating anthropogenic foods, their main prey (e.g., deer, *Odocoileus virginianus*, and elk, *Cervus canadensis*) may become overabundant, causing heavy browsing that affects woody plants, bank erosion, and stream morphology. Original images are courtesy of the Integration and Application Network, University of Maryland.

(Stirling and Derocher 2012). This habitat shift has been linked to modified interactions both among polar bears (e.g., increased rates of infanticide by nutritionally stressed males; Stirling and Derocher 2012) and with other species (e.g., elevated predation on birds, Prop et al. 2015; heightened competition with brown bears, *U. arctos*, Miller S et al. 2015). It has also been associated with elevated polar bear-human conflict. For example, over a three-decade period at Churchill, Manitoba, earlier ice-breakup dates in western Hudson Bay were accompanied by an increase in the number of problem bears (Townes et al. 2009). Accordingly, and especially given that continued Arctic warming is forecasted, climate-driven conflict between polar bears and humans is likely to increase. Much of this conflict will stem from close bear-human contact and the potential for habituation near areas where anthropogenic subsidies are reliably available.

Hybridization and urban carnivores. Since the British colonization of the Americas (in approximately 1600), the distribution and population size of the gray wolf have been greatly reduced, largely because of direct persecution but

also because of habitat loss (Ripple et al. 2014). Conversely, coyotes (*Canis latrans*)—typically subordinate mesopredators where wolves are extant—are now expanding their distribution and abundance and adapting to and successfully exploiting human-modified ecosystems (Newsome and Ripple 2015). The reduced access to mates of small and isolated wolf populations likely facilitated mating between wolves and coyotes, particularly in northeastern North America, where there are now distinct hybrid zones (vonHoldt et al. 2016). In these hybrid zones, some coyote populations became more wolf-like because of the infusion of genes affecting body size and skeletal proportions (vonHoldt et al. 2016). Ongoing hybridization is likely where wolves persist at low numbers, but access to anthropogenic resources in human-modified environments could increase the probability of non-aggressive contact between the two species. This scenario is plausible because coyotes survive and thrive in urban and fragmented landscapes (Fedriani et al. 2001, Gehrt et al. 2011), and wolves are known to use urban fringes and make forays into human settlements to obtain human-provided foods, such as garbage (Ciucci et al. 1997). However, a study in urban Chicago, Illinois,

indicated that anthropogenic foods make up a small proportion of coyote diet (less than 5%; Gehrt et al. 2011), so contact between wolves and coyotes may depend on the level of dietary overlap and wild prey availability. The extent to which wolves will actually occupy urban areas is also unclear, because this ultimately depends on human tolerance (Treves and Bonacic 2016). Studies on mountain lions (*Puma concolor*) demonstrate that large carnivores can persist in fragmented urban landscapes, although selection or use of urban areas appears to be highest for females in comparison with males, and mountain lions appear to adopt behaviors that reduce encounters and potential conflicts with humans (Benson et al. 2016).

The broader consequences for wolves and humans

How do we predict the outcomes for gray wolves when they become heavily reliant on anthropogenic foods? Several viable hypotheses can be derived from the case studies highlighted above. First, the extensive use of anthropogenic foods by wolves in human-dominated landscapes is likely to result in changes to group sizes, diets, home ranges, and sociality, as has been demonstrated in dingoes, red foxes, and bears. These changes are often accompanied by disrupted ecological relationships (e.g., differential use of wild prey; Newsome et al. 2015). Accordingly, their documentation would raise questions about (a) how broadly insights into the role played by wolves gleaned from protected areas such as Yellowstone can be applied in areas that have been grossly modified by humans and (b) the extent to which wolf recolonization can facilitate ecosystem restoration.

Second, although gray wolves move freely in anthropogenic habitats, the survival rates and causes of mortality of wolves in these systems will likely differ from those in less disturbed settings. Rates of population increase could maximize with abundant food resources, but in combination with likely increased human-wolf conflicts and therefore greater human persecution of wolf populations, observed rates of increase could become negative, as has occurred in a case study on bears (Beckmann and Lackey 2008). In support of the latter possibility, a recent study of three wolf populations in the northwest United States showed that although anthropogenic mortality was partly compensatory, it became increasingly pronounced and additive in areas where wolves had the highest exposure to humans and livestock (Murray et al. 2010). Therefore, the gradient from wildlands to human-dominated landscapes is likely to be characterized by a shift from predominantly non-human to anthropogenic mortality of wolves. This switch may lead to lower wolf densities, but it should not preclude the emergence of a commensal canid.

Third, the continued use of anthropogenic foods by gray wolves could result in evolutionary divergence, as in the case of dingoes (Newsome et al. 2013) and red foxes (Wandeler et al. 2003). The commensal process by which wolves appear to have first embarked on the pathway to domestication

was likely followed by a period of purposeful and accidental selective breeding for simple beneficial traits, such as tameness (Trut et al. 2009) and the digestion of starches associated with the domestication of grain-producing plants (Axelsson et al. 2013), and more intensive active selection for beneficial traits, such as coursing, herding, asset protection, and hunting. More recently, humans have bred dogs for aesthetic values, all of which in turn resulted in the diversity of breeds that exists today. There is growing agreement, however, that the process of wolf domestication had advanced considerably prior to the onset of directed breeding (Larson et al. 2012). Therefore, there is no need to invoke artificial selection as a basis for hypothesizing that human-associated wolves are likely to diverge from those subsisting on more natural foods. Rather, as in the Late Pleistocene, when founder groups of less fearful wolves moved toward nomadic encampments to scavenge kills (Driscoll et al. 2009), natural selection and genetic drift would be expected to begin to differentiate wolves relying on human foods from their autonomous counterparts. Accordingly, if extant wolves continue to increase their reliance on anthropogenic foods, we should expect to observe evidence of dietary niche differentiation and, over time, the development of genetic structure that could signal incipient speciation. Niche segregation driven by social or ecological forcing may commonly herald incipient speciation, even at local scales and within populations in which gene flow appears to be unimpeded (e.g., Wolf JB et al. 2008).

Fourth, natural hybridization can lead to speciation or incorporation of new, often suboptimal genes into wild populations (Mallet 2007). Anthropogenic habitat modifications and resource subsidies are likely to increase the opportunity for hybridization. In addition to the wolf and coyote hybrids mentioned above, there are reports of wolves naturally crossing with domestic dogs (Vilà et al. 2003). Domestic dogs are often free ranging and ubiquitous, and reproductive isolation from wolves is unlikely in regions where they co-occur (Vilà et al. 2003). The opportunity for genetic drift and founder effects (e.g., Italian wolf \times dog hybrids) will possibly lead to domestication, as has occurred on more than one occasion previously (Frantz et al. 2016). Contrarily, Verardi and colleagues (2006) cautioned that such natural introgression of dog genes into the wolf genome is rare and their persistence is likely mitigated by ethological constraints. Nevertheless, new wild derivatives of wolf \times dog and wolf \times coyote hybridizations will likely be different behaviorally because their brains and body sizes will differ from those of their parents (Saetre et al. 2004, vonHoldt et al. 2016).

The increasing use of anthropogenic subsidies by gray wolves also has implications for human welfare and conservation policy. Given the persistence of antiwolf sentiment in areas shared by humans and these canids (e.g., Dressel et al. 2015), scenarios of close coexistence similar to those observed between humans and Asiatic lions (see above) are

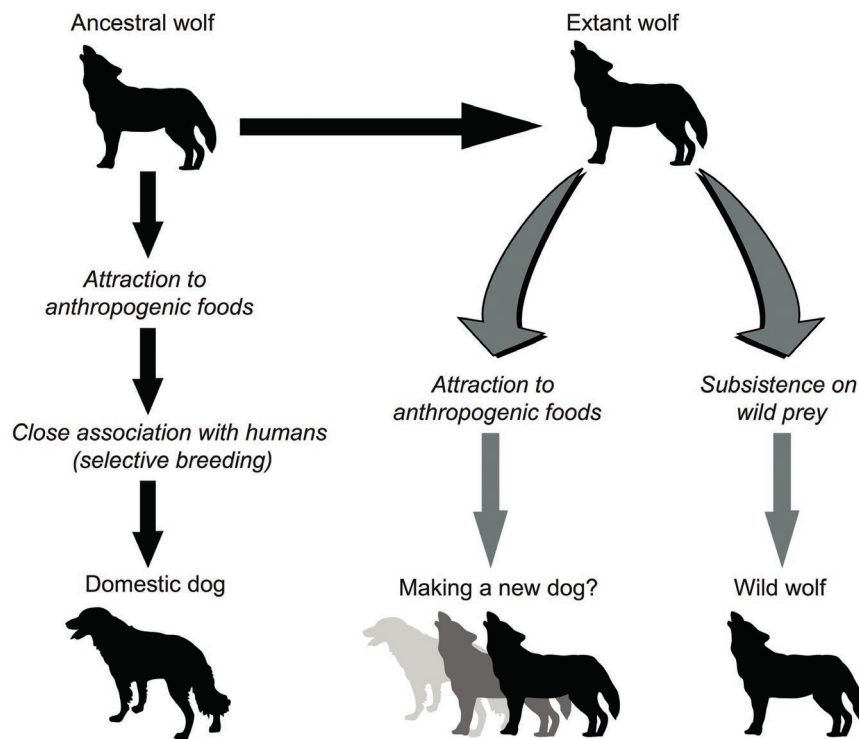


Figure 3. A conceptual model describing the role of anthropogenic foods in the hypothesized original wolf domestication pathway (left) and possible evolutionary divergence (right) due to behavioral and genetic differentiation. Silhouettes are courtesy of Phylopic (Tracy A. Heath).

unlikely to develop. However, in areas where humans provide food to wolves, close encounters are likely to become more frequent, and these encounters could exacerbate conflict. Furthermore, rates of livestock and pet depredation are likely to rise in areas where wolves rely heavily on human foods relative to those observed for wolves in more natural settings. Beyond their economic, human, and animal-welfare implications, these trends would be a cause of concern from a conservation standpoint, given that livestock and pets act as lightning rods for conflict between humans and large predators (Ripple et al. 2014) and indicate the need for changes in how human waste and other resources are managed (e.g., Bino et al. 2010). Finally, given that the depletion of natural prey appears to exacerbate the use of human resource subsidies by wolves (and potentially other large carnivores; see Wolf C and Ripple 2016), we propose that heavy reliance on human foods should be taken as an indicator of ecosystem degradation and should consequently motivate restoration efforts to repatriate landscapes with wild ungulates (especially where suitable habitat exists or where habitat can be restored).

Conclusions

Given that gray wolves have a broad geographic distribution and are recolonizing landscapes around the globe, we are

in the fortunate position of being able to rigorously compare the ecology and genetics of wolves in human-modified and relatively pristine landscapes (e.g., Dorresteijn et al. 2015). Of particular value, in our opinion, would be studies showing the niche characteristics and population structure of wolves in areas where human influence is pervasive and heavy reliance on human foods has been documented, such as in parts of Europe (Chapron et al. 2014, Kuijper et al. 2016, Newsome et al. 2016). In these areas, we might expect to find evidence of nascent niche variation among packs that is explained by access to human resource subsidies and perhaps even the beginnings of genetic differentiation between populations (figure 3). Studies of this nature would allow us to revisit the commensal hypothesis for wolf domestication and postulate what new canid might result in our human-dominated world. We might be able to ask, that is, whether heavy reliance of anthropogenic subsidies can act as a driver of evolutionary divergence and, potentially, provide the makings of a new dog.

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References cited

- Axelsson E, Ratnakumar A, Arendt M-L, Maqbool K, Webster MT, Perloski M, Liberg O, Arnemo JM, Hedhammar Å, Lindblad-Toh K. 2013. The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature* 495: 360–364.
- Banerjee K, Jhala YV, Chauhan KS, Dave CV. 2013. Living with lions: The economics of coexistence in the Gir Forests, India. *PLOS ONE* 8 (art. e49457).
- Baril LM. 2009. Change in Deciduous Woody Vegetation, Implications of Increased Willow (*Salix* spp.) Growth for Bird Species Diversity and Willow Species Composition in and around Yellowstone National Park's Northern Range. Master's thesis. Montana State University, Bozeman.
- Beckmann JB, Lackey CW. 2008. Carnivores, urban landscapes, and longitudinal studies: A case history of black bears. *Human–Wildlife Conflicts* 2: 168–174.
- Benson JF, Sikich JA, Riley SPD. 2016. Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban–wildland gradient. *PLOS ONE* 11 (art. e0158006).
- Bino G, Dolev A, Yosha D, Guter A, King R, Saltz D, Kark S. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology* 47: 1262–1271.
- Chapron G, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1518–1519.
- Ciucci P, Boitani L, Francisci F, Andreoli G. 1997. Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology* 243: 803–819.

- Creel S, Christianson D, Liley S, Winnie JA. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315: 960.
- Crowther MS, Fillios M, Colman N, and Letnic M. 2015. An updated description of the Australian dingo (*Canis Dingo* Meyer, 1793). *Journal of Zoology* 293: 192–203.
- Dorresteijn I, Schultner J, Nimmo DG, Fischer J, Hanspach J, Kuemmerle T, Kehoe L, Ritchie EG. 2015. Incorporating anthropogenic effects into trophic ecology: Predator–prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B* 282 (art. 20151602).
- Dressel S, Sandström C, Ericsson G. 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology* 29: 565–574.
- Driscoll CA, Macdonald DW, O'Brien SJ. 2009. From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences* 106: 9971–9978.
- Elmhagen B, Rushton SP. 2007. Trophic control of mesopredators in terrestrial ecosystems: Top-down or bottom-up? *Ecology Letters* 10: 197–206.
- Fedriani JM, Fuller TK, Sauvajot RM. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24: 325–331.
- Frantz LAF, et al. 2016. Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science* 352: 1228–1231.
- Gehrt SD, Brown JL, Anchor C. 2011. Is the urban coyote a misanthropic synanthrope? The case from Chicago. *Cities and the Environment (CATE)* 4 (art. 3).
- Hosseini-Zavarei F, Farhadinia MS, Beheshti-Zavareh M, Abdoli A. 2013. Predation by grey wolf on wild ungulates and livestock in central Iran. *Journal of Zoology* 290: 127–134.
- Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jędrzejewska B. 2013. Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* 36: 1263–1275.
- Kuijper DPJ, Sahlén E, Elmhagen B, Chamaillé-Jammes S, Sand H, Lone K, Cromsigt JPM. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B* 283 (art. 20161625).
- Larson G, et al. 2012. Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences* 109: 8878–8883.
- Li Y, Wang G-D, Wang M-S, Irwin DM, Wu D-D, Zhang Y-P. 2014. Domestication of the dog from the wolf was promoted by enhanced excitatory synaptic plasticity: A hypothesis. *Genome Biology and Evolution* 6: 3115–3121.
- Lopez-Bao JV, Sazatornil V, Llana L, Rodriguez A. 2013. Indirect effects of heathland conservation and wolf persistence of contradictory policies that threaten traditional free-ranging horse husbandry. *Conservation Letters* 6: 448–455.
- Mallet J. 2007. Hybrid speciation. *Nature* 446: 279–283.
- Meena V, Macdonald DW, Montgomery RA. 2014. Managing success: Asiatic lion conservation, interface problems and peoples' perceptions in the Gir Protected Area. *Biological Conservation* 174: 120–126.
- Migli D, Youlatos D, Iliopoulos Y. 2005. Winter food habits of wolves in central Greece. *Journal of Biological Research* 4: 217–220.
- Miller BJ, Harlow HJ, Harlow TS, Biggins D, Ripple WJ. 2012. Trophic cascades linking wolves (*Canis lupus*), coyotes (*Canis latrans*), and small mammals. *Canadian Journal of Zoology* 90: 70–78.
- Miller S, Wilder J, Wilson RR. 2015. Polar bear–grizzly bear interactions during the autumn open-water period in Alaska. *Journal of Mammalogy* 96: 1317–1325.
- Murray DL, et al. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. *Biological Conservation* 143: 2514–2524.
- Newsome TM, Ripple WJ. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology* 84: 49–59.
- Newsome TM, Stephens D, Ballard G-A, Dickman CR, Fleming PJS. 2013. Genetic profile of dingoes (*Canis lupus dingo*) and free-roaming domestic dogs (*C. l. familiaris*) in the Tanami Desert, Australia. *Wildlife Research* 40: 196–206.
- Newsome TM, Ballard G-A, Crowther MS, Fleming PJS, Dickman CR. 2014. Dietary niche overlap of free-roaming dingoes and domestic dogs: The role of human-provided food. *Journal of Mammalogy* 95: 392–403.
- Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2015. The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography* 24: 1–11.
- Newsome TM, et al. 2016. Food habits of the world's grey wolves. *Mammal Review* 46: 255–269.
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* 16: 1501–1514.
- Packer C. 2013. Is India's pride actually African? *Science* 340: 1289–1290.
- Painter LE, Beschta RL, Larsen EJ, Ripple WJ. 2014. After long-term decline, are aspen recovering in northern Yellowstone? *Forest Ecology and Management* 329: 108–117.
- Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344 (art. 1246752).
- Price EO. 1984. Behavioral aspects of animal domestication. *Quarterly Review of Biology* 59: 1–32.
- Prop J, et al. 2015. Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution* 3: 1–12.
- Ripple WJ, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343 (art. 1241484).
- Saetre P, Lindberg J, Leonard JA, Olsson K, Pettersson U, Ellegren H, Bergström TF, Vilà C, Jazin E. 2004. From wild wolf to domestic dog: Gene expression changes in the brain. *Molecular Brain Research* 126: 198–206.
- Sidorovich VE, Tikhomirova LL, Jędrzejewska B. 2003. Wolf *Canis lupus* numbers, diet and damage to livestock in relation to hunting and ungulate abundance in northeastern Belarus during 1990–2000. *Wildlife Biology* 9: 103–111.
- Smith DW, Tyers DB. 2008. The beavers of Yellowstone. *Yellowstone Science* 16: 4–14.
- Stirling I, Derocher AE. 2012. Effects of climate warming on polar bears: A review of the evidence. *Global Change Biology* 18: 2694–2706.
- Tourani M, Moqanaki EM, Boitani L, Ciucci P. 2014. Anthropogenic effects on the feeding habits of wolves in an altered arid landscape of central Iran. *Mammalia* 78: 117–121.
- Towns L, Derocher AE, Stirling I, Lunn NJ, Hedman D. 2009. Spatial and temporal patterns of problem polar bears in Churchill, Manitoba. *Polar Biology* 32: 1529–1537.
- Treves A, Bonacic C. 2016. Humanity's dual response to dogs and wolves. *Trends in Ecology and Evolution* 31: 489–491.
- Trut L, Oskina I, Kharlamova A. 2009. Animal evolution during domestication: The domesticated fox as a model. *BioEssays* 31: 349–360.
- Verardi A, Lucchini V, Randi E. 2006. Detecting introgressive hybridization between free-ranging domestic dogs and wild wolves (*Canis lupus*) by admixture linkage disequilibrium analysis. *Molecular Ecology* 15: 2845–2855.
- Vilà C, Walker C, Sundqvist A-K, Flagstad Ø, Andersone Z, Casulli A, Kojola I, Valdmann H, Halverson J, Ellegren H. 2003. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf–dog hybrids. *Heredity* 90: 17–24.
- VonHoldt BM, Kays R, Pollinger JP, Wayne RK. 2016. Admixture mapping identifies introgressed genomic regions in North American canids. *Molecular Ecology* 25: 2443–2453.
- Wandeler P, Funk SM, Lurgiader CR, Gloor S, Breitenmoser U. 2003. The city-fox phenomenon: Genetic consequences of a recent colonization of urban habitat. *Molecular Ecology* 12: 647–656.

- Wilmers CC, Crabtree RL, Smith DW, Murphy KM, Getz WM. 2003. Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72: 909–916.
- Wolf JB, Harrod C, Brunner S, Salazar S, Trillmich F, Tautz D. 2008. Tracing early stages of species differentiation: Ecological, morphological and genetic divergence of Galápagos sea lion populations. *BMC Evolutionary Biology* 8: 1–14.
- Wolf C, Ripple WJ. 2016. Prey depletion as a threat to the world's large carnivores. *Royal Society Open Science* 3 (art. 160252).
- Zelder MA. 2012. Pathways to animal domestication. Pages 227–259 in Gepts P, Famula TR, Bettinger RL, Brush SB, Damania AB, McGuire PE, Qualset CO, eds. *Biodiversity in Agriculture: Domestication, Evolution and Sustainability*. Cambridge University Press.

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