

Science & Society

Humanity's Dual Response to Dogs and Wolves

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Dogs were first domesticated 31 000–41 000 years ago. Humanity has experienced ecological costs and benefits from interactions with dogs and wolves. We propose that humans inherited a dual response of attraction or aversion that expresses itself independently to domestic and wild canids. The dual response has had far-reaching consequences for the ecology and evolution of all three taxa, including today's global 'ecological paw print' of 1 billion dogs and recent eradications of wolves.

Our Long History of Relationships with Dogs and Wolves

Dogs, *Canis lupus familiaris*, and wolves, *Canis lupus*, are behaviorally and phenotypically very similar, as we would expect from their close genetic relatedness [1]. However, human societies attach dramatically different cultural symbols to the two canids [2–4]. A landmark in human prehistory was close interaction with some individual wolves that allowed people to select those that were initially less fearful of people or less aggressive to them than others (i.e., taming [5]). The transition, whatever its nature, from competitors to commensals seems to have occurred >41 000 years ago by translating radiocarbon years into actual years [6,7] or 31 000 years ago by genetic dating [1]. Thus, dogs evolved long before other species were transformed by domestication. The origins of tame wolves deserve scrutiny by evolutionary biologists and ecologists for at least three reasons. First, 1 billion dogs

have spread globally [8], leaving a tremendous 'ecological paw print'. Second, scientists have measured coevolved cognitive abilities of humans and dogs [5,9]. Third, wolves were nearly driven extinct across vast areas of their historical range, an eradication that has been linked to domestic animals, including dogs, in complex ways that we explore below. Here we propose a testable hypothesis that explains the origins and consequences of our current mutualism with dogs.

We hypothesize there is an inherited, biological component to human responses to dogs, wolves, and perhaps other canids. The shared evolutionary history of humans, dogs, and wolves produced a dual response in people, from being passionate about one or both to fearful of one or both. The inherited cognitive responses include aversion to members of the dog family (Canidae) as competitors, disease vectors, or predators, as well as a more recent evolved attraction to canids as companions or helpers. To advance this hypothesis, we assume that the precursor to taming wolves was attraction to physical proximity to them.

Physical attraction to wolves might seem risky today but forager societies probably had good reasons. For example, in the Native American Ojibwe creation story, wolf tracks indicated where to find enough deer to support people [2]. Numerous forager societies gain status or ritual power through possessing carnivore remains, with wolves prominent among the artifacts [6]. Therefore, we assume that attraction to wolves and proto-dogs (those lineages of wolves that would become dogs) conferred advantages on humans. Genetic data support the assumption because dogs spread worldwide along with humans in a relatively brief period of <30 000 years [1,6]. Careful examination of the ecological consequences of commensalism with proto-dogs reveals the logic behind our hypothesis of a dual response to canids.

Trends

The massive 'ecological paw print' of 1 billion dogs worldwide can be illuminated by understanding the evolutionary ecology of human–dog mutualism.

We propose a dual-response hypothesis to explain humanity's unusual mutualism with dogs and its competition with wild wolves.

Our hypothesis makes testable predictions for the fields of psychology, genetics, and political ecology.

Benefits of early commensalism with proto-dogs might have included earlier warning of danger, intimidating human and nonhuman competitors, companionship, increasing the efficiency of prey detection or capture, or transport of materials by pulling travois or carrying saddlebags [4]. However, these early benefits do not necessarily explain acceptance by other people within the tamer's community who lacked the attraction to canids. Presumably a commensal relationship between tamer and proto-dog required that the tamer also convinced associates to tolerate these proto-dogs and their young in frequent, close physical proximity. Tolerance would be required because there would also be costs of commensalism with proto-dogs.

Costs of the nascent commensalism would arise because proto-dogs might have increased the frequency of encounters with wild wolves or their pathogens. Seasonal reproductive cycles might have regularly and predictably attracted wolves to proto-dogs and led proto-dogs to search for wolf mates. Therefore, we assume elevated probabilities of attacks on humans and infections (e.g., rabies), at least until people invented surgical sterilization or eradicated local wolves. Repeated mixing of wild wolves and proto-dogs might set back the artificial selection for tameness and incidentally obscure the genetic origins of dogs. Evidence for forms intermediate between wild wolves and proto-dogs exist in the fossil record [7]. Furthermore, the above

incursions and setbacks in tameness would presumably generate animosity to proto-dogs and wolves among associates of the tamers. People who felt cautious or fearful towards canids might have helped some communities to reduce the costs of proximity to wolves and proto-dogs. We hypothesize that avoidance led to stabilizing selection for a polymorphism of attraction to or avoidance of one or both canids at least initially in human prehistory. It might also have spurred social conflict between individual people expressing different genetic (and learned) responses to canids.

A key event in the evolution, ecology, and social conflict might have been the domestication of livestock, if livestock attracted wolves nearer to people or led proto-dogs to prey on livestock. Because both dogs and wolves have long been blamed for threats to human safety and damage to other animals [10,11], the domestication of livestock might have triggered both eradication efforts against wolves and pressures to select dogs that were useful around livestock, such as breeds that protect or herd livestock (Figure 1A,B). The cultural transmission and refinement of domestication practices might have arisen from a positive feedback loop in which artificial selection of dog breeds advanced the domestication process for other animals and vice versa (citing G. Larson; [12]). Eventually special dog breeds that bond to livestock rather than to people were invented, which seems to enhance the mutualism between humans and dogs (Figure 1A,B). We predict that societies dependent on livestock faced more recent, destabilizing selection for greater attraction to dogs and less to wolves.

The persistence and persuasiveness of negative symbolism of wolves (e.g., Little Red Riding Hood) would presumably be weighed against that of positive symbolism (e.g., Remus and Romulus) as societies experienced the net benefits minus costs of both wild and domestic canids.



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Figure 1. (A) A Livestock-Guarding Dog Protects Sheep in Slovenia. These dog breeds bond to livestock and spend all of their time with them rather than bonding to humans. (B) The same dog charging the photographer as he approached. Photographs: Dr M. Krofel.

Members of cultures that expressed strong pro-dog and strong anti-wolf reactions would be expected to take the dual response to an extreme. For example, Euro-American bear hunters who use hounds in Wisconsin hold the most anti-wolf attitudes we have documented despite currently living near Native American Ojibwe who descend from forager societies and hold the most positive

attitudes towards wolves we have ever measured [11,13]. Extreme social norms include open promotion of illegal wolf killing in Wisconsin [14] and protecting the rights of dogs to roam without restraint in Chile (Supreme Court ruling on case 210172-2015 available on request).

In contrast to the Biophilia hypothesis [15], our dual-response hypothesis helps to

Box 1. Testable Predictions of the Dual-Response Hypothesis

Cognitive scientists should be able to detect and disentangle human reactions to various canid stimuli as evidence of a dual response. For example, presenting four stimuli associated with aggressive or playful canids in a two-by-two treatment using stimuli unambiguously associated with either wolves or dogs could elicit any of four distinct responses depending on an observer's genetic makeup.

The inherited, biological components of aversion or attraction to canids might be expressed in young children exposed to puppies or dog-like stimuli. One should look for reactions that are instinctive responses (i.e., expressed in functional or mature form at first stimulus).

The relative abundances of dogs and wolves as well as their roles in human society are dictated even today by a sociopolitical negotiation among people of different phenotypes that is mediated by local benefits minus costs perceived by power elites, interest groups, and society at large. Social scientists and ecologists can help to relate current mutualisms to historical patterns of interaction with canids.

explain variation in attraction to canids. We made only three assumptions: the precursor to taming was attraction to wild wolves; mutualism was adaptive; and different responses to one or both canids were heritable. We predict that humans today exhibit four distinct phenotypes: either pro- or anti-either dogs or wild canids. Our hypothesis makes testable predictions (Box 1). We offer the dual-response hypothesis to help explain the massive ecological influence of dogs today and the repeated local extinctions of wolves and various wolf-like animals, including the Malvinas fox, *Dusicyon australis*, and the marsupial thylacine wolf, *Thylacinus cynocephalus*. The dual-response hypothesis also generates at least three testable predictions for several fields of science (Box 1).

Society and Narrow-Interest Groups

Human-dog mutualism has led to the global spread of dogs [8], with an associated widespread and deep ecological paw print. Meanwhile, wolves have been driven

extinct in many regions globally and only legally enforceable conservation efforts during the past 40 years have prevented continental extinctions. Whether wolves vanish or recover will reflect social conflicts over the value of wolves. Narrow-interest groups such as Chile's pro-dog organizations and the US anti-wolf organizations mentioned above can occasionally drive societies into extreme positions on dogs or wolves. Likewise, moderate interest groups may push back against extremes to restore mutualisms with dogs that make sense ecologically and ethically and reestablish a coexistence with wild wolves that makes sense as well. Humanity's dual responses help to explain modern ecological and social conflicts over dogs and wolves.

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