

Chasing the Tale

Origins of the Human–Dog Relationship

Dogs evolved from wolves.¹ This evolutionary transformation occurred in the company of humans through a process of interspecies symbiosis. The numerous breeds purposely developed by humans, as well as human individual and collective actions that are less organized, suggest that the decisions and actions of *Homo sapiens* now largely determine dog evolution. Quite possibly, our millennia of close association with dogs have also affected our own evolution, perhaps predisposing us toward valuing their presence in our lives. But when did the transformation of wolf into dog get started, and how has it evolved over time? What specific economic concepts and models help us understand how and why the symbiosis developed? And what biological and sociocultural forces have sustained it across both time and space? We address these questions as a prelude to our treatment of the economics of dogs in our modern lives.

2.1 SNIFFING OUT THE BEGINNING: THE ARCHAEOLOGICAL (AND NOW GENETIC) EVIDENCE

The genetic and archaeological evidence suggests that the close human-canine association emerged more than 20 thousand years ago, somewhere in Eurasia. We advisedly use the broad and somewhat vague term “close association,” at least at this point. The word association allows

¹ Genetic evidence suggests that after an initial flow of genes from wolves to dogs, what further flow occurred tended to be from dogs back to wolves. Anders Bergström, Laurent Frantz, Ryan Schmidt, Erik Ersmark, Ophélie Lebrasseur, Linus Girdland-Flink, Audrey T. Lin et al. “Origins and Genetic Legacy of Prehistoric Dogs.” *Science* 370, no. 6516 (2020): 557–564.

us to sidestep somewhat both the evolutionary processes by which the association arose and its exact nature within an evolutionary perspective. Biologists usually divide symbiosis – any close relationship between two species where at least one of the species benefits – into three forms: mutualism, commensalism, and parasitism.² With mutualism, both species benefit from the relationship; with commensalism, one species benefits and the other species neither benefits nor is harmed (i.e., it bears no evolutionary relevant cost); and with parasitism, one species benefits and the other species is harmed (e.g., as in the interaction between dogs and roundworms). Evolutionary biologists have empirically shown that the form of symbiosis can evolve over time, at least at the bacterial level.³

To the extent that economics, and especially the applied economics that is of most relevance to dog-related policies, regulation, and markets, primarily concerns itself with contemporary and expected future margins of human behavior, we could largely ignore the evolutionary and biological causal factors that underlie our cross-species association. Thus, the primary focus of this chapter is on what we consider to be the basic economics of the human–canine interaction. Although we do not dive deeply into the genesis of how the association arose, we do dangle our toes. We do so because economic concepts and methods – most specifically ideas from game theory – have played an important role in structuring theory and empirical research around basic evolutionary, and related, questions. We also do so because causal factors, however far back in time they arose, help us think about human and dog interactional behaviors in the present.

Genetic evidence suggests that the domestic dog (*Canis lupus familiaris*) diverged from the gray wolf (*Canis lupus*) as long ago as 100 thousand years somewhere in East Asia.⁴ However, the earliest archeological evidence of domesticated canids (beyond just association) is found further west and only around 14 thousand years ago.⁵ Even then, the relationship was complex and multidimensional; Luc Janssens and his

² Aparajita Das and Ajit Varma. “Symbiosis: The Art of Living.” In Ajit Varma and Amit C. Kharkwal, eds., *Symbiotic Fungi, Soil Biology* 18 (Berlin, DE: Springer-Verlag, 2009), 1–28.

³ Paul Herrera, Lisa Schuster, Cecilia Wentrup, Lena König, Thomas Kempinger, Hyunsoo Na, Jasmin Schwarz et al. “Molecular Causes of an Evolutionary Shift along the Parasitism–Mutualism Continuum in a Bacterial Symbiont.” *Proceedings of the National Academy of Sciences* 117, no. 35 (2020): 21658–21666.

⁴ Xiaoming Wang and Richard H. Tedford. “Evolutionary History of Canids.” In Per Jensen, ed., *The Behavioural Biology of Dogs* (Cambridge, MA: CABI, 2007), 3–20.

⁵ Darcy F. Morey. *Dogs: Domestication and the Development of a Social Bond* (New York, NY: Cambridge University Press, 2010).

colleagues present poignant evidence of early humans caring for a very sick young dog that had almost no chance of survival without their care.⁶

2.2 HOW DID WE DOMESTICATE DOGS ... OR HOW DID WE DOMESTICATE EACH OTHER?

How might the close association have evolved? Kayla Stoy and her colleagues point out that “Despite the ubiquity and importance of mutualistic interactions, we know little about the evolutionary genetics underlying their long-term persistence.”⁷ Biologists do have some suggestive evidence about how genetic temporal processes work from bacterial symbiosis; but that is very far from symbiosis between more complex organisms. Thus, behavioralists of all stripes have considered a wide range of other kinds of evidence, including indirect evidence of biological processes by observing the results of selective breeding of dogs, of the closely related fox, and of other domesticated animals, as well as contemporary interactions between species. After reviewing these interesting questions and some of the alternative hypothesizes about the genesis of the human–dog association, we focus on economic theory, and related evidence, that might help explain, or at least interpret, interspecies symbiosis. We should keep in mind that we are not claiming or describing genetic comingling between species, so while we think this terminology is informative, it is to some extent metaphorical. In that vein, Edward O. Wilson uses the term “social symbiosis.”⁸ However, as we discuss in the next section, while there is no interspecies gene mixing, humans have clearly and repeatedly influenced the canine genetic makeup.

Biologists have documented many examples of symbiosis between species ranging from aphids and ants to honey guides and humans. Charles Darwin described the convincing evidence of the ubiquity of symbiosis as one of the most serious challenges to the theory of evolution.⁹

⁶ Luc Janssens, Liane Giemisch, Ralf Schmitz, Martin Street, Stefan Van Dongen, and Philippe Crombé. “A New Look at an Old Dog: Bonn-Oberkassel Reconsidered.” *Journal of Archaeological Science* 92, April (2018): 126–138.

⁷ Kayla S. Stoy, Amanda K. Gibson, Nicole M. Gerardo, and Levi T. Morran. “A Need to Consider the Evolutionary Genetics of Host–Symbiont Mutualisms.” *Journal of Evolutionary Biology* 33, no. 12 (2020): 1656–1668 at 1656.

⁸ Edward O. Wilson. *Sociobiology: The New Synthesis* (Cambridge, MA: Harvard University Press, 2000).

⁹ There is some disagreement among evolutionary biologists on whether symbiosis still represents a serious challenge to the neo-Darwinism synthesis (the standard contemporary version of Darwinism incorporating modern genetics, as represented by John

To help understand the evolution of interspecies symbiosis, biologists after Darwin's era have drawn on game theory, a basic tool of economics, and the other social sciences.¹⁰ The resulting framework, evolutionary game theory, is now a widely used approach to studying intraspecies evolution, interspecies symbiosis, and even the prevalence of social norms among humans.¹¹ Although it would take us too far afield to provide more than a cursory discussion of evolutionary game theory, we think brief introductions to classical and evolutionary game theories are useful in understanding how cooperation between people and wolves might have originally arisen and been sustained. Before considering game theory models related to the emergence of mutualistic symbiosis (the relationship in which we assume *Homo sapiens* and dogs now coexist), we briefly review the explanations that have been offered for the origin of domestication.

2.3 POSSIBLE EXPLANATIONS FOR THE EARLY STAGES OF DOMESTICATION

What use is a dog? To man, that is. To consider this difficult and contentious question, we draw on two studies that summarize most of the alternative hypotheses. In discussing these hypotheses, some biologists distinguish between what they call utilitarian motivation hypotheses and others they describe as nonutilitarian motives;¹² this is something we

Maynard Smith and Richard Dawkins). For the case that it does, see Lynn Margulis and David Bermudes. "Symbiosis as a Mechanism of Evolution: Status of Cell Symbiosis Theory." *Symbiosis* 1, no. 2 (1985): 101–124. For an accessible discussion of the importance of the idea that symbiosis is different, see Bradford Harris. "Evolution's Other Narrative." *American Scientist* 101, no. 6 (2013): 410. For a very balanced assessment, see Maureen A. O'Malley. "Endosymbiosis and Its Implications for Evolutionary Theory." *Proceedings of the National Academy of Sciences* 112, no. 33 (2015): 10270–10277.

¹⁰ Seminal works include John Maynard Smith and George R. Price. "The Logic of Animal Conflict." *Nature* 246, no. 5427 (1973): 15–18; John Maynard Smith. "The Theory of Games and the Evolution of Animal Conflicts." *Journal of Theoretical Biology* 47, no. 1 (1974): 209–221 and John Maynard Smith. *Evolution and the Theory of Games* (New York, NY: Cambridge University Press, 1982).

¹¹ H. Peyton Young. "The Evolution of Social Norms." *Annual Review of Economics* 7, no. 1 (2015): 359–387.

¹² Luc A. A. Janssens and Dennis F. Lawler. "The Earliest Domesticated Wolves: On Creating Dogs." In Sabine Gaudzinski-Windheuser and Olaf Jöris, eds., *The Beef Behind All Possible Pasts the Tandem-Festschrift in Honour of Elaine Turner and Martin Street, Volume 2* (Mainz, DE: Verlag des Römisch-Germanischen Zentralmuseums, 2021), 485–504.

return to later in this chapter (and in a later chapter) but using different terminology for reasons we explain. C. Clyde Manwell and C. M. Ann Baker summarize ten possible canine domestication scenarios (partly in the context of Australian indigenous populations and dingoes).¹³ Because these domestication scenarios do not exclusively assume the domestication of wolf puppies (but rather dingoes and other potential hybrid proto-canids), here we use the broader label “canid domestication.” These scenarios are not mutually exclusive explanations.

Manwell and Baker pose what we identify as the following ten scenarios. First, canids could have provided value to humans as auxiliary hunters. Their value as hunting partners rests on both a similarity and difference. Dogs and humans have comparable endurance, which allows them to cooperate over long distances. However, canids have a much better sense of smell than humans, a useful complement to hunting. We can expect canids to share the same functions in hunting that archaeologists have identified for dogs. These include locating and encountering prey, indicating specific locations of prey, restricting the movement of prey, and pursuing and recovering prey.¹⁴

Second, canids could have come into contact with humans by being either big or small game “kill thieves.” When humans made large game kills, especially during the “Pleistocene Overkill,” which hypothesized that humans hunted megafauna to extinction,¹⁵ they often had a temporary abundance of food that could not always be guarded against canid larceny. Canids would also have been able to outrace humans to small game killed with primitive missile weapons. (Readers who have had dogs know that many still have some larceny in their hearts: your authors have witnessed otherwise well-behaved dogs give in to the temptation to grab blocks of cheese, and once even a whole ham, from tables!) The possibility of opportunities for such larceny would have conditioned some canids to seek to be near humans.

Third, canids could have served as guards or sentinels for the clan because of sensory complementarities with humans. Although humans

¹³ C. Clyde Manwell and C. M. Ann Baker. “Domestication of the Dog: Hunter, Food, Bed-warmer, or Emotional Object?” *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 101, no. 1–5 (1984): 241–256.

¹⁴ See Angela R. Perri. “Prehistoric Dogs as Hunting Tools: The Advent of Animal Biotechnology.” In Brandi Bethke and Amanda Burtt, eds., *Dogs: Archaeology Beyond Domestication* (Gainesville, FL: University Press of Florida, 2020), 7–44.

¹⁵ Todd A. Surovell, Spencer R. Pelton, Richard Anderson-Sprecher, and Adam D. Myers. “Test of Martin’s Overkill Hypothesis Using Radiocarbon Dates on Extinct Megafauna.” *Proceedings of the National Academy of Sciences* 113, no. 4 (2016): 886–891.

generally have better day and night vision, canids tend to have better vision at dawn and twilight. More importantly, canids have keener senses of smell and hearing than humans, enabling them to detect the presence of animals that humans cannot see. Along with better senses of smell and hearing, shorter spells of REM sleep would have made canids especially valuable sentinels at night. They also would have had the capability to directly interdict smaller intruders.

Fourth, canids could have acted as auxiliary fighters in early intrahuman conflicts or possibly *Homo sapiens*' conflicts with Neanderthals or Denisovans. Beyond the especially valuable role of sentinel in conflict situations, canids could directly attack enemies with teeth and claws or intimidate them with growls. History offers many descriptions of dogs engaging in this function – and even as recently as the sixteenth-century conquistadors deployed war dogs against the native peoples of the New World.¹⁶

Fifth, the canid could have served as a human food source (the “edible dog” in Manwell and Baker’s terminology). Stationary clans might very well have captured or raised canids as a regular food source, just as dogs are a food source today in some Asian countries. However, canids might have been more valuable as a reserve food source. Sharing kills with canids may have been done explicitly as a means of storing food. It also may have been just an expedient strategy in times of scarcity. Relatedly, it is known that the indigenous peoples of the north-west coast of North America kept dogs for the use of their hair in clothing.

Sixth, women could have engaged in heterospecific suckling of canids. It is reasonable to assume that women in early human clans experienced high rates of infant mortality so that there would often be lactating women who had no infants to feed. Consequently, it is possible that abandoned or orphaned canid pups might be introduced to the clan and then adopted by women who had lost infants. The sucking would likely have created a bond between the pup and the women that could have resulted in the canid staying with the clan into adulthood. The heterospecific suckling of dogs and pigs has been documented in a geographically wide range of contemporary societies, consistent with the possibility of its role in canid domestication.¹⁷

¹⁶ For an account of the gruesome use of war dogs by the conquistadors, as well as dogs as more benign characters in historical events, see Stanley Coren. *The Pawprints of History: Dogs and the Course of Human Events* (New York, NY: Free Press, 2002).

¹⁷ Frederick J. Simoons and James A. Baldwin. “Breast-Feeding of Animals by Women: Its Socio-Cultural Context and Geographic Occurrence.” *Anthropos* 77, no. 3/4 (1982): 421–448.

Seventh, the canid could have served as a bed warmer, or more generally, participate in interspecies huddling in the presence of extreme cold. Participants in huddling effectively reduce their ratios of surface area to volume, reducing their losses of body heat. The huddling is mutually beneficial for both the canids and the humans. One can imagine that reliance on huddling may have reduced the amount of bedding required, which would have been valuable to clans that changed locations frequently: canids were effectively self-propelled bedding. Manwell and Baker speculate that bed warming might have been the earliest source of domestication.

Eighth, canids could have contributed to cleansing campsites by serving as scavengers. Rather than thieving game, canids may have been invited to eat food remains, especially those unpalatable for humans, to help avoid rodent and insect infestations. (In contrast to this indirect rodent control through sanitation, it is likely that cats began associating with humans after agriculture permitted the storage of grain that attracted rodents.¹⁸)

Ninth, canids could have played an important role in transportation. Although their capacity for directly carrying loads is relatively small, they would have effectively pulled sleds in regions with substantial snow or ice. Dogs still pull sleds for some northern clans today. One reason that they have maintained this role despite the domestication of draft animals is that they can share food with humans. We might speculate that Ernest Shackleton's South Pole expedition would have fared much better if it employed more dogs than ponies.

Tenth, canids could have become emotional objects for humans. The emotional link may have arisen from human engagement with young animals, whether as a consequence of heterospecific suckling or through other contact. Or it may have been a byproduct of associating with canids preforming other functions. Manwell and Baker write: "The presence of an animal strongly integrated with cultural traditions of a people, succoured at considerable cost, yet seemingly devoid of economic implications, has resulted in speculations over a variety of aesthetic, religious, ceremonial or psychological functions for animals."¹⁹

Luc A. A. Janssens and Dennis F. Lawler posit a number of motivational reasons that are very similar to those presented by Manwell and

¹⁸ Carlos A. Driscoll, Juliet Clutton-Brock, Andrew C. Kitchener, and Stephen J. O'Brien. "The Taming of the Cat." *Scientific American* 300, no. 6 (2009): 68–75.

¹⁹ Manwell and Baker, p. 250.

Baker and so we see no need to repeat them, but they also distinguish between two underlying mechanisms; either collection of (very young) wolves or some other canid pups or through self-domestication.²⁰ From a game-theoretic (and evolutionary) perspective, the distinction between pup collection and self-domestication is potentially important because self-domestication-related hypotheses lend themselves more readily to a transition to mutualistic symbiosis, while puppy collection is more akin to parasitism or commensalism (the latter being the case where wolf puppies suffer from abandonment unrelated to humans).

2.4 INSIGHTS FROM CLASSICAL GAME THEORY

Game theory is widely utilized in the social sciences, especially in economics, where it has now become one of the primary frameworks for graduate training. Although it has evolved considerably since its introduction in the 1940s, we refer to its contemporary use in the social sciences as classical game theory. This distinguishes it from evolutionary game theory, which shifts focus from the strategic behavior of individuals to competition among strategies inherent in individuals, such as through genetics in the case of studies of the evolution of species or social norms in the case of human interaction. Each of these game-theoretic frameworks offers some insights that are useful for thinking about canine domestication.

In classical game theory, a game specifies players, their strategies, payoffs jointly conditional on selected strategies, and their knowledge of the strategies and payoffs. Here, we focus our attention on what are called non-cooperative games, which assume that the players cannot make binding commitments about the strategies they will play. Social scientists, mathematicians, and (as we will see) biologists have developed a wide range of games, as well as various ways of classifying them. The strategies are then tested against each other, mostly in controlled experimental (laboratory) settings. This allows for systemic variation in the parameters of the game, such as the payoffs and available information. This is very convenient and potentially informative! However, we have to keep the limitations of such games in mind when extrapolating their results to actual human and animal behaviors and especially to the interaction between humans and other species.

²⁰ Janssens and Lawler, pp. 491–492.

Stage Game: Played One Time

		Pack Strategies	
		Share (S)	Hoard (H)
Clan Strategies	Share (S)	2,2	-1,3
	Hoard (H)	3,-1	0,0

Equilibrium: (H,H)

Repeated Game: Stage Game Repeated with Probability p

Some possible equilibria in repeated game:

1. Clan and Pack always hoard.

(H,H)(H,H)(H,H)...

2. Clan and Pack share in first round and then continue sharing as long as the other player shared on the last round. If either player hoards, the other never shares again. This strategy in the repeated game is an equilibrium if and only if the probability of playing another round of the stage game is sufficiently large ($p > 1/3$):

(S,S)(S,S)(S,S)...

FIGURE 2.1 Hunting Game (prisoner's dilemma): Single round and repeated

The situation most relevant to our current interest is the game displayed in Figure 2.1. It considers a game that can be played either once or multiple times – following conventional usage, we refer to the basic structure of the game played one time as the *stage game* and the multiple rounds of play of the stage game as the *repeated game*. The table within Figure 2.1 displays the players, strategies, and payoffs for the stage game. For our initial purposes, we label it as the Hunting Game, although, as our earlier discussion indicated, hunting is only one of a number of equally plausible, or perhaps even more plausible, other explanations. Readers familiar with game theory will recognize the Hunting Game as a particular example of the Prisoner's Dilemma game, which famously illustrates how individuals rationally seeking to maximize their own payoffs can lead to social inefficiency.

In our version of the Prisoner's Dilemma game, we label one player the "Clan," and the other, the "Pack," for *Homo sapiens* and wolves, respectively. The Clan and the Pack each has two possible (mutually exclusive) strategies, "Share" or "Hoard." Share means that the Clan or the Pack cooperates in hunting big prey and sharing the resulting food (protein and fat). Hoard means that a player does not cooperate.

The payoffs to the players are given in the cells of the two-by-two table of strategies with the first number showing the payoff to the Clan and the second number showing the payoff to the Pack. So, for example, if the Clan hoards and the Pack shares, the Clan gets a positive payoff of 3 units of food and the Pack gets none of the kill and loses the equivalent of 1 unit of food from uncompensated effort. To predict the outcome of the Hunting Game, we identify combinations of strategies of the players that are *Nash equilibria* in the sense that neither player could increase its payoff by unilaterally changing its strategy.

We first assume that the stage game will only be played once. When the game is played only once, an inspection of the table of payoffs displayed in Figure 2.1 should make it clear why both players decide to engage in hoarding (H,H). This is an equilibrium because, if the other player is hoarding, unilaterally moving to sharing would reduce food payoffs from 0 to -1. Indeed, it turns out that (H,H) is the only equilibrium – which one can verify by identifying desirable changes in strategies for one or both players for any of the other strategy combinations. We can see why other strategies when the game is played only once are not equilibria. For example, one player sharing and the other hoarding, that is, either (S,H) or (H,S), is not an equilibrium because the sharing player could unilaterally increase its payoff from -1 to 0 units of food by changing strategies to hoarding. Both players sharing (S,S) is also not an equilibrium because either player could increase its payoff from 2 to 3 units of food by switching to hoarding. Thus, even though (S,S) would potentially give each player a higher payoff than (H,H), it is not an equilibrium and therefore unlikely to occur. It is this divergence between the equilibrium of mutual hoarding and the more desirable outcome that would result from mutual sharing that makes this game structure so interesting to social scientists. Although a Clan and a Pack randomly encountering each other would benefit from sharing in a big game hunt (S,S) and so maximize their food gains, their individual incentives would be to hoard so that the predicted outcome would be the equilibrium (H,H).

Next assume that there is repeated interaction rather than one-time play of the stage game. This repeated interaction might occur because of some degree of colocation; this becomes more likely as the number of clans, or wolf packs, or both, increase over time. If some clans and packs do settle near each other to permit repeated interaction, then the possibility for a cooperative equilibrium arises. The model of repeated

cooperation shown in Figure 2.1 assumes that the stage game is repeated in successive rounds with a probability of p . That is, after playing the stage game, the probability of playing it again is p . Strategies in this repeated game are defined as choices of stage game strategies conditional on what has occurred in previous rounds of play. Equilibrium strategies in the repeated game involving sharing by a clan and a pack are possible if the probability of playing another round of the stage game is sufficiently high.

For example, consider the following strategy in a repeated game: share in the first round and continue sharing if the other player shared in the previous round. If the other player hoards, then hoard in all future rounds. Both players following this strategy will be an equilibrium if the expected payoff to each player of following the strategy is greater than ever hoarding. If the Clan and the Pack each follow this strategy, then the expected payoffs are $2(1 + p + p^2 + p^3 + \dots)$, which equals an expected $2/(1 - p)$ units of food. Hoarding in the first round would earn a payoff of 3 units of food, but 0 unit in all future rounds. The sharing strategy will be an equilibrium if $2/(1 - p) > 3$, or $p > 1/3$. This illustrates that, if the probability of repeated interaction is sufficiently high, then mutual sharing (S,S) in each round is an equilibrium in the repeated game and therefore a plausible prediction of strategy choices and outcomes.

This strategy, however, is only one of the possible equilibria in this repeated game. Other sharing equilibria could also exist in the presence of large enough values of p . For example, one famous and highly intuitive strategy is known as “tit for tat.”²¹ In this strategy one player starts off by sharing in the first round and then copying what the other player did on the previous round. A tit-for-tat strategy should result in sharing if p is sufficiently large.²² Indeed, unlike an unforgiving strategy of punishing a case of hoarding by responding with hoarding ever after, tit for tat opens up the possibility of strategies that embody forgiveness: that is, returning to sharing if one of the players hoarded, whether deliberately or inadvertently. In moving from repeated games

²¹ The somewhat surprising success of the tit-for-tat strategy was made famous in a tournament of different strategies pitted against each other in the repeated prisoner’s dilemma game. See Robert Axelrod, *The Evolution of Cooperation* (New York, NY: Basic Books, 1984).

²² The so-called Folk Theorem indicates that repeated games usually have an infinite number of “cooperative” equilibria. See Drew Fudenberg and Eric Maskin. “The Folk Theorem in Repeated Games with Discounting or Incomplete Information.” *Econometrica* 54, no. 3 (1986): 533–554.

with two players to multiplayer games, tit for tat may provide some degree of robustness of sharing even in the presence of hoarding by a single player.

Note that in a game with only a single equilibrium like the Hunting Game, if players know the number of repeated interactions with certainty, then a cooperative equilibrium of mutual sharing is not possible. We deduce this by backward induction, through which each player would have an incentive to switch to hoard in the last round. Anticipating hoarding in the last round, the players would have an incentive to hoard in the penultimate round. This process would unravel mutual sharing. To sustain the equilibrium of mutual sharing, there must always be a positive probability of playing the stage game at least one more time. It may be possible to support cooperative equilibria in stage games repeated a fixed number of times if there are more than one equilibrium.

How plausible is it that such sharing could evolve? For it to occur, a clan and pack must first interact in some way. One can imagine a number of reasons why clans and packs might tend to colocate as a precursor to interaction. Many reasons would relate to the attraction of locations with reliable supplies of water and adequate tree cover; this is a strong driver of species colocation in spatial environments with uneven resource endowments. More related to associational behavior, wolves are effective (and often apex) scavengers in colder climates. The Pack would find it beneficial to eat parts of kills that clans do not consume in situations when food is plentiful (and not storable); the Clan may benefit from fewer rodents if the wolves clean up – a source of canid and human association we have already noted.

It is also possible that sharing arose through some more idiosyncratic circumstances such as a clan and pack cornering the same mastodon and sharing in the abundance that a very large carcass provides. This could provide a context for a first round of sharing that might then be repeated to mutual benefit.²³ These scenarios imply that sharing could somehow continue. Assuming foresight and memory by clans, one way of getting to repetition is to assume foresight and memory by particular packs; some research does suggest that wolves as well as dogs may have an

²³ On the limitations of explaining mutual animal behavior with such games, see Nichola J. Raihani and R. Bshary. “Resolving the Iterated Prisoner’s Dilemma: Theory and Reality.” *Journal of Evolutionary Biology* 24, no. 8 (2011): 1628–1639.

aversion to inequality, suggesting a social awareness potentially relevant to reciprocity.²⁴

More generally, how plausible are games as models of either animal or interspecies interaction? Although not directly relevant to the evolution of cooperation between humans and canines, a detour to the question of what we know about whether, and if so how, animals play games may help us assess the plausibility of game-theoretic explanations of animal behavior. We are specifically interested here in these questions from the perspective of the findings from experimental game theory, which have been conducted in two different contexts. The first context is whether some animals appear to play games with humans. The second context is intraspecies interaction between individual members of some nonhuman species. In both contexts, most of this research has been conducted with various primate species.

Both contexts raise a fascinating underlying question: are interactions (and so games) between members of nonhuman species different from the same kinds of interactions between humans? A starting point for thinking about capacity to play games is the cognitive trade-off hypothesis.²⁵ This hypothesis conjectures that the brains of different species specialize in different capabilities – which economists would frame as different species having different absolute and comparative advantages.²⁶ In humans, cortical growth has evolved around language and categorization. Both are extremely valuable to humans, at the expense of other capacities that are better retained by other species, such as detailed perception and pattern recognition. These capacities are critical for many species in their intraspecies social

²⁴ See Jennifer L. Essler, Sarah Marshall-Pescini, and Friederike Range. “Domestication Does Not Explain the Presence of Inequity Aversion in Dogs.” *Current Biology* 27, no. 12 (2017): 1861–1865. For an overview of the research on inequality aversion in dogs, see Jim McGettrick and Friederike Range. “Inequity Aversion in Dogs: A Review.” *Learning & Behavior* 46, no. 4 (2018): 479–500.

²⁵ Elsa Adessi and her colleagues discuss how nonhuman animals “think” about economics given their cognitive abilities and limitations. Elsa Adessi, Michael J. Beran, Sacha Bourgeois-Gironde, Sarah F. Brosnan, and Jean-Baptiste Leca. “Are the Roots of Human Economic Systems Shared with Non-human Primates?” *Neuroscience & Biobehavioral Reviews* 109 (2020): 1–15.

²⁶ A comparison of similarly raised wolf and dog pups shows the genetic basis for cognitive differences between these species. Eniko Kubinyi, Zsófia Virányi, and Ádám Miklósi. “Comparative Social Cognition: From Wolf and Dog to Humans.” *Comparative Cognition & Behavior Reviews* 2 (2007): 26–46.

interaction in the absence of language or for competitive activities such as hunting.²⁷ In intraspecies games, the evidence shows that a range of primates can play cooperatively.²⁸ Regarding primate games against humans, the experimental evidence shows that in some games chimpanzees do as well as humans, and, in some pattern recognition games, they do better.²⁹

2.5 INSIGHTS FROM EVOLUTIONARY GAME THEORY

A framing of interspecies interaction that is clearly more consistent with the requirements of evolutionary theory, however, would be that some wolves had a genetic trait that predisposed them to share. Rather than modeling individual rationality in the choice of strategies, from this perspective one models the success of strategies. John M. Smith was one of the pioneers of this approach to modeling evolution, now called evolutionary game theory.³⁰ Rather than individual players choosing strategies, the players have genetically endowed strategies. Some strategies will mutate and replicate in some circumstances. The primary focus is on identifying *evolutionarily stable strategies* (ESS). ESSs are such that if they are present in the whole population, they cannot be successfully invaded by a mutant strategy that then persists in the population.

Biologists typically model evolutionary change with dynamic versions of evolutionary game theory that simulate genetic changes over time (and sometimes space). The most common approach models interactions among members of the population such that those who gain relatively more resources from their interactions with other members have more offspring.³¹ Computer simulation methods, such as agent-based models, allow researchers to assess the dynamics of evolutionary change in more

²⁷ Christopher F. Martin, Rahul Bhui, Peter Bossaerts, Tetsuro Matsuzawa, and Colin Camerer. “Chimpanzee Choice Rates in Competitive Games Match Equilibrium Game Theory Predictions.” *Scientific Reports* 4, no. 1 (2014): 1–6.

²⁸ Gillian L. Vale, Lawrence E. Williams, Steven J. Schapiro, Susan P. Lambeth, and Sarah F. Brosnan. “Responses to Economic Games of Cooperation and Conflict in Squirrel Monkeys (*Saimiri boliviensis*).” *Animal Behavior and Cognition* 6, no. 1 (2019): 32–47.

²⁹ Martin et al.

³⁰ John M. Smith. *Evolution and the Theory of Games* (New York, NY: Cambridge University Press, 1982).

³¹ Carlos P. Roca, José A. Cuesta, and Angel Sánchez. “Evolutionary Game Theory: Temporal and Spatial Effects beyond Replicator Dynamics.” *Physics of Life Reviews* 6, no. 4 (2009): 208–249.

		Player 2 Strategies	
		Hawk (H)	Dove (D)
Player 1 Strategies	Hawk (H)	$(V-C)/2, (V-C)/2$	$V, 0$
	Dove (D)	$0, V$	$V/2, V/2$

Pure Strategy Stage Game Equilibria: (H,D) and (D,H)

Mixed Strategy Stage Game Equilibrium: Play H with probability V/C

Neither pure strategy is an ESS; mixed strategy is an ESS.

FIGURE 2.2 Hawk–dove game with high costs of fighting ($C > V$)

complex models than can be solved mathematically.³² However, for our purposes, the simple static version of evolutionary game theory provides an adequate introduction to the basic approach.

In the Hunting Game example shown in Figure 2.1, mutual hoarding is also an ESS because if all individuals are genetically predisposed to hoard, it will be impossible for an individual with the sharing mutation to successfully invade the hoarder population. A sharing invader would consistently lose, both absolutely and relative to the incumbent hoarding population. The possibility of an ESS that allows multiple genetic strategies (called “mixed strategies”) requires a game with multiple equilibria.

A canonical example in evolutionary game theory that features equilibria resulting in the survival of a diversity of genetic strategies is the Hawk–Dove game in which the players are seeking some resource and bear a cost in competing or fighting for it. In the Hawk–Dove game, the possible strategies are to be either a Hawk – threatening and fighting if resisted – or a Dove – backing down when threatened (in Monty Python parlance “run away”). The relevant features of the Hawk–Dove game are shown in Figure 2.2 for the case in which the cost of fighting (C) exceeds the value of the resource (V) – if V were greater than C , then the game would be similar to the Hunting Game in which there is only one equilibrium, which would be (H,H) in this case. We can interpret the Hawk–Dove game from the perspective of classical game theory. Doing so, there are three equilibria. Two of these equilibria, (H,D) and (D,H), are pure strategies like the equilibrium as in the Hunting Game, while the third is a mixed equilibrium that involves the players randomizing their strategies such that there

³² For an overview of the use of agent-based simulation models for investigating more complex evolutionary processes, see Christoph Adami, Jory Schossau, and Arend Hintze. “Evolutionary Game Theory Using Agent-Based Methods.” *Physics of Life Reviews* 19 (2016): 1–26.

is a probability of V/C of playing H and a probability of $(1 - V/C)$ of playing D.³³

Now we switch from classical game theory back to an evolutionary game perspective in which individual players are not making purposive switches in strategies, but instead mutate from an initial strategy to a new one. In doing so, we can show why neither of the two pure strategies would be ESS. To see why, imagine that everyone in the population is an H. It would be possible for a D to invade and replicate by gaining a higher payoff. However, if the entire population became D, then an H could invade and replicate. This same logic applies when the population includes some mix of H and D individuals. Assume that the proportion of H individuals in the population is q and therefore the proportion of C individuals is $1 - q$. A mutation of an H to a D would replicate or survive if it increased the mutant's expected payoff. The expected payoff to being an H is $q[(V - C)/2] + (1 - q)V$. The expected payoff from mutating to a D is $q(0) + (1 - q)V/2$. But some algebra shows that $q[(V - C)/2] + (1 - q)V < q(0) + (1 - q)V/2$ only if $q > V/C$. A similar calculation shows that mutating from C to H increases the expected payoff only if $q < V/C$. Only when the genetic endowment of H and C in the population corresponds to the mixed strategy would there be no opportunity to survive and successfully replicate – an ESS only results when the likelihood of an H meeting a D is equal to V/C .

We can think of a game of this sort as representing the genetic “strategy” of some individual wolves in a wolf pack “deciding” whether to associate with humans, such that associating and not associating have payoffs as in the Hawk–Dove game: it is better to not associate if food can simply be taken from those humans who do acquire it. The mixed strategy equilibrium corresponds to an ESS that requires the existence of both associating and nonassociating types of wolves within the wolf population. Wolves who do associate are those that are more genetically susceptible to domestication and becoming dogs, while those who do not are predisposed to remain wolves.

2.6 INDUCED MUTATION

It is common to think of genetic change for mammals as occurring over relatively long periods of time. One might therefore expect that any

³³ The mixed strategy assigns probabilities to the pure strategies for each player such that the other player has the same expected payoff from either of its strategies.

genetic mutations in wolves that would be significant enough to affect the propensity to be domesticated would be very slow to accumulate and require numerous generations of wolves or proto-dogs. However, recent experience with intensive selective breeding suggests that this is not necessarily the case. Experiments in Russia with captive foxes that have little associative behavior with humans have shown that it can be induced through selective breeding.³⁴ “Starting from what amounted to a population of wild foxes, within six generations (6 years for these foxes, as they reproduce annually), selection for tameness, and tameness alone, produced a subset of foxes that licked the hand of experimenters, could be picked up and petted, whined when humans departed, and wagged their tails when humans approached. An astonishingly fast transformation.”³⁵ Furthermore, any resulting genetic and epigenetic changes in the foxes are driven by human (mainly economic) motivational forces rather than by neo-Darwinian replication forces.³⁶ These results from the selective breeding of foxes make fairly rapid genetic changes that moved wolves toward dogs plausible: humans may have adopted relatively associative wolves and bred them to produce even more associative wolves that noticeably evolved toward dogs within human lifetimes.

From the human perspective, devoting resources for the care of dogs might have been evolutionarily costly. One explanation for the human attachment to dogs is that dogs take advantage of human responses that evolved to facilitate interaction with other humans. Evolving an appearance more like human babies and evolving behaviors that encouraged humans to impute familiar mental processes to dogs enabled the dogs to secure resources from humans.³⁷ As the functional value of dogs developed, humans who evolved to be more accepting of dogs would have gained an advantage. From this perspective, dogs evolved from parasite to mutualists. We next turn to the economics of clans keeping dogs.

³⁴ Lee A. Dugatkin, Lyudmila Trut, and Liudmila N. Trut. *How to Tame a Fox (and Build a Dog): Visionary Scientists and a Siberian Tale of Jump-started Evolution* (Chicago, IL: University of Chicago Press, 2017). Also see Lyudmila N. Trut. “Early Canid Domestication: The Farm-Fox Experiment.” *Scientificur* 24, no. 2 (2000): 124.

³⁵ Lee A. Dugatkin. “The Silver Fox Domestication Experiment.” *Evolution: Education and Outreach* 11, no. 1 (2018): 1–5 at 2.

³⁶ Dean Lueck and Gustavo Torrens. “Property Rights and Domestication.” *Journal of Institutional Economics* 16, no. 2 (2020): 199–215.

³⁷ John Archer. “Why Do People Love Their Pets?” *Evolution and Human Behavior* 18, no. 4 (1997): 237–259.

2.7 DOGS ONCE IN THE CLAN: THE ECONOMICS OF DOG COPRODUCTION

Early human clans most likely viewed dogs both as companions and productive resources.³⁸ (In economic terminology, the companionship would be considered a consumption value and therefore dogs would be considered to be consumption goods.) Figures 2.3 and 2.4 illustrate the implications of dogs having some value in production of goods as well. As a starting point, Figure 2.3 displays the unlikely situation in which dogs have only companionship value – perhaps adopted cute puppies that become simply companions. The vertical axis indicates the quantity of goods, other than dogs, such as food, clothing, and leisure that the clan consumes, whereas the horizontal axis represents the number of dogs that the clan keeps.

Consuming either dog companionship or other goods involves a cost. Leisure must be given up to secure other goods (an *opportunity cost*) and consuming the companionship of dogs involves a cost in terms of sharing food with them and spending time caring for them beyond the value of the companionship from interaction. For illustrative purposes, imagine that all other goods and dogs each have a constant per unit “price” in terms of time needed to secure them. The clan has a fixed amount of total available time. If the clan spends all of its time on acquiring other goods, then it could consume G_m , but it must do so without any dogs. Alternatively, although this is obviously not advisable if the clan hopes to survive, the

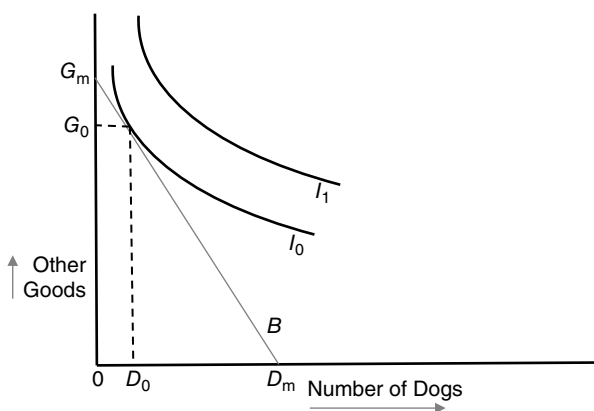


FIGURE 2.3 Dogs as companions

³⁸ On goods that contribute to both consumption and production, see Wing Suen and Pak H. Mo. “Simple Analytics of Productive Consumption.” *Journal of Political Economy* 102, no. 2 (1994): 372–383.

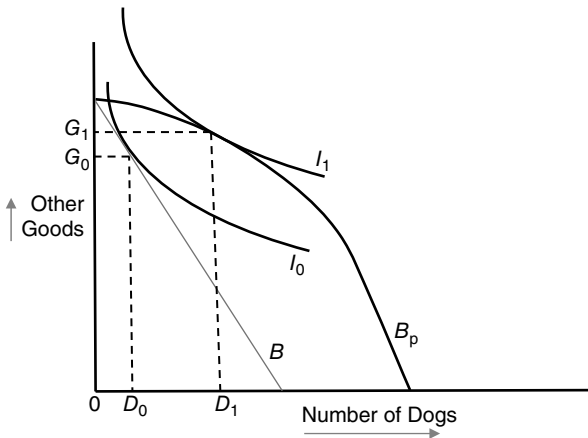


FIGURE 2.4 Dogs as companions and productive resources

Source: Adapted from Wing Suen and Pak H. Mo. "Simple Analytics of Productive Consumption." *Journal of Political Economy* 102, no. 2 (1994): 372–383, Figure 1.

clan could spend all of its time on acquiring dogs, and so consuming the companionship of D_m dogs. The line connecting these points, labeled B , represents a budget constraint that indicates the possible combinations of companion of dogs and other goods that the clan could consume.

The various combinations of dogs and other goods each give the clan some levels of utility, or satisfaction. All possible combinations allow us to construct an index of satisfaction. The higher the index value, the greater is the level of satisfaction. As the clan would like more of all goods including dogs, points in the space further to the northeast in Figure 2.3 give higher levels of satisfaction. Different combinations of companion dogs and other goods can provide the same level of satisfaction. The curves labeled I_0 and I_1 are *indifference curves* that show such combinations. If the clan has coherent preferences, then a family of indifference curves like I_0 and I_1 exists; they do not intersect, and they lie either closer or further from the origin marked o . I_0 is drawn to be just tangent to the budget constraint and is the indifference curve offering the highest level of satisfaction that the clan can achieve with budget constraint B ; it results in consumption of D_0 companion dogs and G_0 other goods.

Figure 2.4 illustrates the consequences of dogs also having productive value for the clan. For example, assume that the clan uses dogs in hunting or guarding the camp at night. Or perhaps the dogs contribute directly to consumption by providing warmth on cold nights that makes sleep

more pleasant (hence a very cold “three dog night”). These contributions to production thus shift the budget constraint further to the northeast as more dogs join the clan, increasing consumption possibilities. Now the clan can reach indifference curve I_1 , an indifference curve that offers a higher level of clan satisfaction than was possible if dogs offer just companionship. With the added production of dogs, the clan can consume dog companionship D_1 , a greater amount than the D_0 consumed if dogs were not productive. It can also consume more of other goods as well: G_1 is greater than G_0 .

2.8 INCENTIVES FOR THE CREATION OF BREEDS

Economic models explain species mutualism in terms of “biological markets” in which the species can trade resources.³⁹ As in economic models of international trade in which comparative advantage enables both countries to gain from specialization in production, comparative advantage may facilitate specialization that expands the resources available to the species through mutualism. We have already considered various ways that canid and humans can benefit from exchange. However, once domestication transformed wolves into dogs, humans had the opportunity to engage in economic selection, a form of artificial selection rather than natural selection.⁴⁰ How can we explain the human motivation to invest resources in creating more productive breeds?

Consider the situation in which dogs are only production inputs (perish the thought!) Figure 2.5, for example, illustrates the role of dogs in sheep herding. The curve labeled B shows benefits as a function of the size of the flock. The curve labeled C_{nd} is the cost a shepherd bears in herding different flock sizes without the assistance of dogs. The point on the horizontal axis labeled Q_{nd} indicates the number of sheep that maximizes the excess of benefits over costs for the shepherd; this difference, or “profit,” is represented by the length of the arrow labeled N_{nd} . The curve labeled C_d is the cost the shepherd bears from working with dogs. For very small flock sizes, working with dogs may actually involve higher

³⁹ Mark W. Schwartz and Jason D. Hoeksema. “Specialization and Resource Trade: Biological Markets as a Model of Mutualisms.” *Ecology* 79, no. 3 (1998): 1029–1038; Peter Hammerstein and Ronald Noë. “Biological Trade and Markets.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 371, no. 1687 (2016): 1–12.

⁴⁰ Carlos A. Driscoll, David W. Macdonald, and Stephen J. O’Brien. “From Wild Animals to Domestic Pets, an Evolutionary View of Domestication.” *Proceedings of the National Academy of Sciences* 106, no. Suppl 1 (2009): 9971–9978.

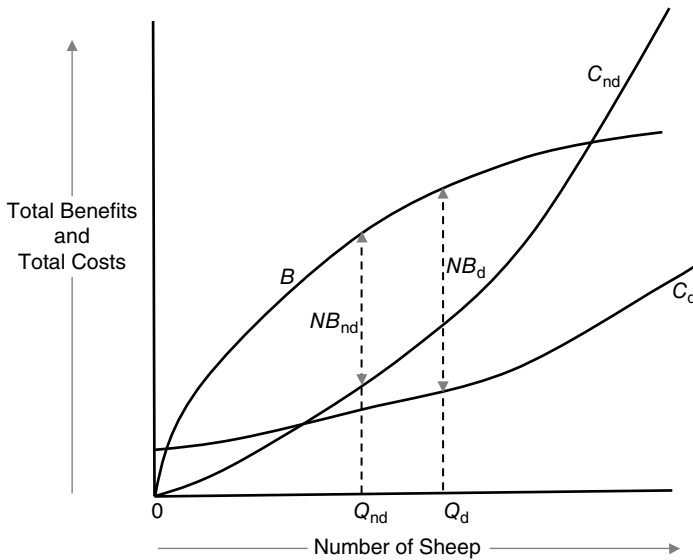


FIGURE 2.5 Human–dog cooperation from the human perspective

cost. However, at some incrementally larger flock size, the increase in the cost of herding with the assistance of dogs falls below that of doing it without dogs. The result is that a larger flock size, labeled Q_d now maximizes the excess of benefits over costs for the shepherd; this difference is represented by the length of the arrow labeled N_d .

The curve labeled C_d assumes the availability of dogs with some level of skill in herding. When dogs first began being used in herding, C_d was likely very close to C_{nd} because of relatively low levels of herding instinct. However, economic selection likely resulted as shepherds kept and bred dogs that were more helpful in herding (and perhaps less prone to eat lamb on their own, which in turn might favor sheep that are less afraid of dogs). This selective breeding would lower C_d , enabling the shepherd to increase “profits” by increasing flock size. Similar economic selection likely operated to create breeds particularly skillful in other productive activities such as hunting and guarding. Indirect economic selection eventually became common as specialists in breeding dogs selected for physical characteristics potential customers found attractive.

2.9 CONCLUSION

Dogs were the first domesticated animal species – our association with domesticated dogs has been so long and widespread that tracing genetic

changes in dogs has proven valuable to archaeologists in tracing the prehistoric migrations of people.⁴¹ Many factors could have encouraged wolves to associate with humans, setting the stage for domestication. As we have tried to show in this chapter, economic perspectives and tools can be helpful in interpreting our long association with dogs. In subsequent chapters, economic perspectives offer much more direct insight into our continuing relationship with our furry friends.

⁴¹ Angela R. Perri, Tatiana R. Feuerborn, Laurent A. F. Frantz, Greger Larson, Ripan S. Malhi, David J. Meltzer, and Kelsey E. Witt. “Dog Domestication and the Dual Dispersal of People and Dogs into the Americas.” *Proceedings of the National Academy of Sciences* 118, no. 6 (2021): 1–8.