



Integrating social ecology in explanations of wolf–dog behavioral differences

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Whereas studies in comparative cognition normally invoke ecology and social organization to account for differences in social behaviour and cognition across species, dog–wolf differences have so far been explained mostly as a result of direct human selection for desirable traits (e.g., tameness, attention to humans, sociability). Yet, as will be reviewed in this paper, dogs and wolves also differ considerably in both their feeding niche and social organization (which together we refer to as ‘social ecology’). We suggest that observed wolf–dog differences especially in their interaction with the environment (e.g., neophobia, persistence, risk taking) and conspecifics (e.g., tolerance, cooperation, communication) need to be considered also in regard to their social ecology. We propose that social ecology alongside human selection should be recognized as a potentially important factor affecting dogs’ behaviour, and suggest a number of potential avenues for future research, which can more directly test the relative importance of these selection forces.

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Introduction

Genetic analyses indisputably conclude that dogs’ closest living relatives are grey wolves suggesting that the common ancestor prior to domestication likely resembled modern day wolves [1]. Pioneering studies by Frank *et al.* in the 1980s [2] and more recent research in Hungary [3] and Austria [4] have highlighted a host of behavioural

differences between wolves and dogs. To account for these differences, a series of ‘dog domestication hypotheses’ have been proposed suggesting that human selection for specific traits such as *increased attention to humans* [5]; *acceptance of humans as social partners* [6]; *reduced fear and aggression of humans* [7]; a *tamer temperament* [8], human-directed *social competence* [9] lead to increased cooperativeness and related cognitive skills in dogs.

Although differing in the specifics, all the hypotheses above (see Ref. [10[•]] for a review) attempt to account for observed differences in wolf–dog behaviour & cognitive skills based solely on direct selection by humans for specific dog traits, which relate to face-to-face interactions with people (we collectively refer to these as the ‘*human-oriented*’ hypotheses). However, the direct interaction with humans is not the only change that occurred during the domestication process, and as we hope to clarify, wolves and dogs differ in a number of other important aspects.

Domestication scenarios: tentative steps back in time

The location of dog domestication is still controversial [11], but it is widely accepted that dogs were well established across Eurasia by the late Pleistocene, that is, before the advent of cultivation. Two scenarios have been proposed for the early stages of dog domestication: the human-selection and the self-domestication scenario.

The ‘*human-selection*’ scenario (or ‘directed pathway’ [12[•]]) postulates that people actively adopted wolf pups and selected only the most docile animals for reproduction [13]. Circumstantial support for this scenario comes from archaeological and anthropological records showing that adoption and taming of various Canid species by indigenous populations occurred across South America before the arrival of domestic dogs [14], suggesting this may have occurred also with wolves.

Differently, the ‘*self-domestication*’ or ‘*commensal pathway*’ hypothesis proposes a two-stage process. In the first stage, dogs’ ancestors started exploiting a new feeding niche provided by humans reducing their reliance on conspecific group hunting and increasing their dependence on human generated food/refuse [12[•],15]. Already at this stage, selective pressures may have acted on proto-dogs’

characteristics with less fearful individuals being more likely to approach human settlements, thus maintaining an advantage in the exploitation of the new niche compared to their more timid conspecifics [8]. Proof of concept that proto-dogs were able to acquire and maintain distinct characteristics despite continued significant gene flow with wolves comes from recent studies of two wolf populations in North America [16,17]. Despite living sympatrically and with regular gene flow between them, these populations have specialized in different prey and habitat use; one adopting a migratory lifestyle (following caribou), the other a more territorial organization dependant on local prey. They also show a suite of genetic and morphological differentiations such as a lighter coat colouring in the migratory population. The second stage of the ‘self-domestication’ hypothesis, proposes that humans then started a direct selection by removing unwanted animals (*e.g.*, too aggressive) and favouring animals with desired characteristics (*e.g.*, more attentive, responsive, cooperative).

Only a time-machine would allow us to determine which scenario occurred, and quite possibly both processes played a role. However, independently of which pathway dogs took during domestication, the feeding niche of today’s wolves and dogs is remarkably different from each other and likely has been since the advent of cultivation.

The feeding ecology and social organization of wolves and dogs

Although the common perception of the ‘dog’ is that of a ‘pet dog’, free-ranging dogs actually represent between 70 and 80% of the world dog population [18,19] and in many areas free-ranging dogs appear to form a quite distinct population deriving from ancestors native to the region rather than a recent admixture of modern breeds (*e.g.* Africa [20]; South and Central Asia, [21]; Eurasia, [22] but [23]). These populations are not, as is often thought, made up of ex-pet dogs (which represent the minority), but rather they are self-sustaining populations of ‘free-breeding’ animals that independently choose their mates [24,25] and whose existence is affected by dispersal patterns, food abundance, mate choice as well as human activities [15,26].

Hence in the remaining part of this review we aim to (1) highlight the differences in the feeding ecology of wolves and free-ranging dogs and, likely as a consequence, (2) in their social organisations; and (3) suggest that to fully explain the behavioural differences between dogs and wolves, their respective social ecologies need to be taken into account.

Feeding ecology

Most wolves predominantly rely on group hunting of ungulates. Both the location and abundance of prey

change seasonally, hence predictability is low. Furthermore, hunting is risky, considering most ungulates have the capacity to seriously injure their attackers. Finally, hunting requires extraordinary persistence considering success rates are only between 10% and 49% [27]. Although the relationship between hunting success and pack size is nonlinear but dependent on prey type [28] and defence from scavengers [29], it appears to play a role both in hunting success and territorial defence [30].

Free-ranging dogs typically live in proximity to human settlements [31] and their survival rates, at least in some areas, are significantly affected by direct human intervention [32]. Their diet consists predominantly of human waste (between 50 and 88%) with grains and human faeces (20%) as major components [33,34]. While hunting (including group hunting) wild animals is part of dogs’ feeding ecology [34,35], in most populations it plays a minor role and occurs mostly if human-provided food sources are not sufficient [36,37] or when dogs live at greater distances from humans [34,38]. The importance of starch, and clear evidence of a shift in feeding ecology from hunting to scavenging, emerges from dogs showing genetic adaptations for starch digestion, which are absent in wolves [39] but already present in the ancient Newgrange dog (4800 BP-11). Scavenging on human refuse appears to be mostly a solitary or dyadic activity [40] likely due to the fact that the food is itemized and dispersed and does not require multiple individuals to obtain it. In fact if more animals are moving together and find the same small resource, it would likely be counterproductive allowing potential for conflict to emerge. Indeed, Ethiopian wolves (also part of the *Canis* genus) show a social structure like that of grey wolves (a bonded pair with offspring), but due to the dispersed, itemized and reduced dimension of their prey, which consists mostly of burrowing rodents, they are mostly solitary foragers, only occasionally showing group hunting of small ungulates [41].

Social organization

Wolf packs are predominantly composed of a breeding pair (which form a long-term bond), their adult and sub-adult offspring as well as pups from the most recent litter [42]. However, unrelated individuals may also join [43]. All members participate in pup-rearing by regurgitating food for the pups (and the lactating female) as well as defence from predators. Pups start actively participating in hunts only at 7–8 months of age; until then they are almost totally reliant on other pack members [44]. Both litter size and pup survival is linked to pack size (and food abundance) [45]. Overall, it appears that wolves are highly reliant on a cohesive and functional pack structure allowing them to successfully forage, defend their territory and raise pups [44].

Table 1

Feeding ecology of wolves and dogs

	Wolves-hunters	Dogs-scavengers
Content	Specialist: meat	Generalist: grain/starch, human faeces
Distribution	One large monopolizable	Small, distributed items
Predictability	Low: seasonal fluctuation/changing location	High: seasonally constant/fixed location
Danger/Risk	High: prey can be dangerous	None
Reliance on conspecifics	High for large prey	None
Human resource dependence	None	High

Free-ranging dogs appear to be ‘facultatively social’, potentially depending on food abundance [26,46], breeding status of females and season [40]. Most studies report that free-ranging dogs form groups of 2–8 individuals although stable packs of up to 27 individuals have also been reported [47]. Packs are multi-male, multi-female, with some females choosing to breed with just one male, but the majority being promiscuous [25]. Pups are raised mostly by their mothers (including regurgitation [47]), although a few cases of paternal and ‘grandmotherly’ care have been observed [48,49]. By the age of 10–11 weeks, mothers no longer provide for them [50]. Pups may remain with their native pack (and having reached sexual maturity breed themselves) or disperse.

Wolf–dog social ecology compared

Interestingly, in both wolves and dogs, there are examples of different feeding strategies being adopted: some wolves have been observed scavenging on human refuse [51] and some dogs cooperatively hunting [34,35]. Similarly, mating strategies may also be flexible to a certain extent, with one example reported in dogs where only a single female was observed breeding in a family pack of feral dogs in Alaska [52] and occasional reports of multiple breeding females in wolf packs [44]. In a number of Canid species, mating strategies appear to vary in accordance with resource abundance/distribution [46,53], highlighting the strong link between feeding ecology and social organization (hence the term ‘social ecology’). Likely this is the case also for grey wolves and dogs; nevertheless, comparing their more typical feeding ecologies (Table 1) and social organizations (Table 2), potentially important differences emerge.

In particular, humans’ long-term food storage capabilities provide waste uniformly over the course of a year and in predictable locations. Free-ranging dogs have adapted to this niche, and reliance on this fairly constant, predictable and safe food source has likely affected all aspects of their social life. Pair-bonding is no longer required since lactating females can den close to the food source [31] and can leave pups alone for only brief periods to forage. This diminishes the need for alloparental investment as pups are rapidly able to provide for themselves [15,18]. As a consequence, dogs’ reliance on pack members for both foraging and pup-rearing is much reduced compared to wolves. We suggest that such differences in social ecology may help explain behavioural differences observed in comparative studies of wolves’ and dogs’ interactions with their social partners and asocial environment.

Experimental studies of wolf–dog differences

Although the major focus of wolf–dog comparative research has been on their interactions with humans [10], there is a growing number of studies also comparing their behaviour with conspecifics and the environment. The actual results appear to be difficult to account for based only on a ‘human-oriented’ view of domestication. Indeed, whereas a direct selection for tameness would predict higher tolerance and therefore higher cooperative abilities in dogs compared to wolves [8], a number of studies have not supported these predictions.

As regards tolerance, compared to wolves, pack-living dogs are less tolerant of proximity during feeding on a monopolizable food source tending to avoid conflict by maintaining distance rather than using communication to negotiate access as wolves do [54,55]. In the same

Table 2

Social organization in wolves and dogs

	Wolves	Dogs
Group composition	Breeding pair + offspring	When in packs: several breeding females, males and offspring
Mating system	Pair bonding	Mostly promiscuous
	Seasonal	Non-seasonal
Parental care	By all pack members	Mostly maternal (some cases of paternal)
Pup dependence on adults	High-prolonged	Low-short lived

populations during daily observations of the animal’s social interactions, we found that low intensity aggressive encounters (not involving physical contact) were more frequent in wolves while higher intensity conflicts (involving physical contact) were more frequent in dogs, with reconciliation occurring in the former but not the latter (Cafazzo *et al.*, submitted); indeed, after conflicts, dog opponents avoided each other by limiting their interactions. From these results it emerges that dogs tend to adopt an avoidance of conflict strategy, which does not however equate to tolerance, since when it comes to food, dominant dogs monopolize the resource more successfully than dominant wolves [55].

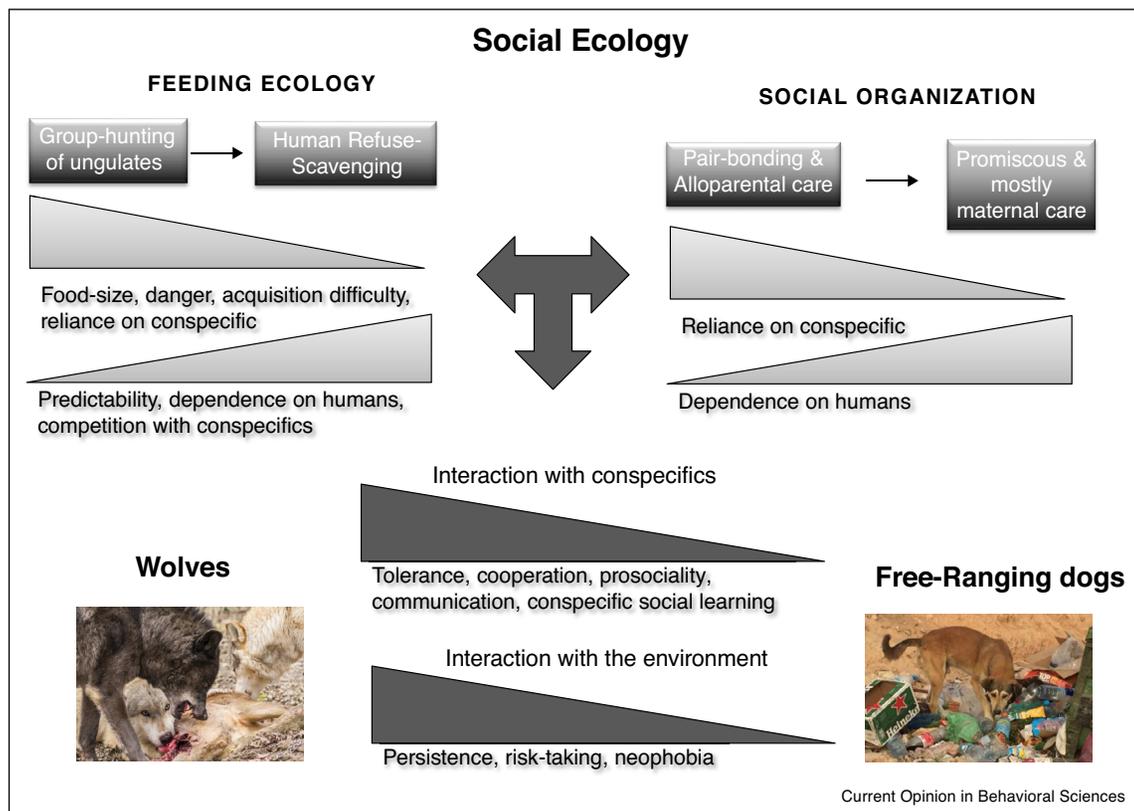
In line with the above, a series of older studies comparing group living wolves and dogs showed that regardless of breed, dogs showed more escalations into serious fighting than wolves [56]. Moreover, in a developmental study, the frequency of agonistic behaviours in dogs was more similar to that of solitary living and scavenging jackals than of wolves [57]. Based on these observations, Feddersen-Petersen [58] suggested that dogs cooperate less than wolves, even at the most basic level of synchronizing their behaviours with conspecifics. Indeed, when

comparing equally raised and kept pack-living wolves and dogs, the latter showed a reduced capacity for imitative learning from a conspecific [59], and were less successful in intraspecific cooperative tasks (Marshall-Pescini *et al.*, submitted).

Taken together, such results are in line with the social ecology of the two species since dogs’ reduced reliance on pack members (for both hunting and pup-rearing) and greater dependence on small dispersed food sources which are sought mostly solitarily, may have relaxed the need for intraspecific communication and tolerance around food sources, as well as the need for social learning abilities and cooperative skills (Figure 1).

Differences have also been found between wolves’ and dogs’ independent problem solving abilities and interactions with their environment. Predictions based on the selection for tamer temperament would be that a reduction in fear would allow them a greater ease/pr propensity to explore and manipulate novel objects/environments [60]. However, results seem to be more in line with the different ecologies of the two species with wolves being more persistent (and successful) in manipulative problem

Figure 1



Changes in the feeding ecology and social organization from wolves to dogs and how these may affect their behaviour towards conspecifics and the environment.

solving tasks [61,62,63] and more risk-prone when given a choice between a safe low quality reward vs. a high quality but less certain one [64]. Furthermore, in line with their more dangerous and complex foraging strategy [65], compared to dogs, wolves are more neophobic, in that they take longer to approach a novel object, but then they spend more time exploring such objects as well as novel environments [66,67] (Figure 1).

Finally, as regards interaction with humans, domestication has without doubt eased the propensity of dogs to accept humans as social partners with very little exposure to humans necessary for dogs to become socialized [68] in contrast to the intensive human contact needed for wolf pup socialization [69]. However, it is interesting to note, that, when acceptance of humans as social partners is achieved, differences between wolves and dogs in understanding social cues and cooperating with them are smaller than initially thought. Indeed, at the Wolf Science Center, where both are similarly extensively socialized to humans, wolves show a similar capacity to socially learn from a human partner [70], are equal to, if not better, at following human gazing cues into distant space and around barriers [71,72] and are as likely to use gaze

Box 1 Future research which may help better understand the effect of wolves' and dogs' social ecology on their observed behavioural differences

Future research

Disentangling the relative role of social ecology and human-selection on dogs' social behaviour and cognition is difficult as there is no dog population where no direct selection by humans has occurred. Nevertheless some areas of research may help to address this question:

(1) Belyeav *et al.* pioneering experiments selecting for tameness in silver foxes resulted in a 'tame' population that can be compared to the original unselected 'control' population [60]. If human-selection affects behaviours towards conspecifics and the environment, differences between control vs. tame foxes should mirror those observed between wolves and dogs.

(2) The resource dispersion hypothesis (RDH, [46]) verified in a number of Canid species predicts that food abundance affects the social organization of different within species populations. Studying multiple free-ranging dog populations with different feeding ecologies and social organizations in relation to their behaviours with conspecifics and the environment may help better understand whether these three factors are indeed linked.

(3) Dingoes are thought to have undergone a lighter process of human selection compared to today's domestic dogs and in many areas continue living in a free-ranging state. A better understanding of the links between their feeding ecology and social organization would provide potentially important insights in the earlier phases of domestication.

(4) Comparing the behaviour with conspecifics and the environment between closely related species (dog, wolves, coyotes, jackals) with differing levels of dependence on group hunting vs. scavenging may provide insights on the effects of feeding ecology on social behaviour.

alternation to gain help from a human in obtaining an out-of-reach reward [73].

Conclusion

In conclusion, we suggest that, although human selection for favourable traits (*e.g.*, tameness, human sociality, attention) played a major role in dog domestication, changes in their social ecology (*i.e.*, both their feeding niche and social organization) may also have played a significant part in moulding dogs' behavioural and cognitive profile and should therefore be integrated in dog domestication hypotheses and given more attention in future research (Box 1).

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest

1. Lindblad-Toh K *et al.*: **Genome sequence, comparative analysis and haplotype structure of the domestic dog.** *Nature* 2005, **438**:803-819.
2. Frank H, Frank M: **The University of Michigan canine information-processing project (1979-1981).** In *Man and Wolf. Advances, Issues, and Problems in Captive Wolf Research.* Edited by Frank H. Dordrecht: Dr. W. Junk Publishers; 1987:143-167.
3. Kubinyi E, Virányi Z, Miklósi A: **Comparative social cognition: from wolf and dog to humans.** *Comp. Cogn. Behav. Rev.* 2007, **2**:26-46.
4. Range F, Virányi Z: **Tracking the evolutionary origins of dog-human cooperation: the 'Canine Cooperation Hypothesis'.** *Front. Psychol.* 2015, **5**:1582 <http://dx.doi.org/10.3389/fpsyg.2014.01582>.
5. Miklósi Á, Kubinyi E, Topál J, Gácsi M, Virányi Z, Csányi V: **A simple reason for a big difference: wolves do not look back at humans, but dogs do.** *Curr. Biol.* 2003, **13**:763-766.
6. Gácsi M, Györi B, Virányi Z, Kubinyi E, Range F, Belényi B, Miklós Adám: **Explaining dog wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills.** *PLoS One* 2009, **4**:e6584 <http://dx.doi.org/10.1371/journal.pone.0006584>.
7. Hare B, Tomasello M: **Human-like social skills in dogs?** *Trends Cogn. Sci.* 2005, **9**:439-444.
8. Hare B, Wobber V, Wrangham R: **The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression.** *Anim. Behav.* 2012, **83**:573-585.
9. Miklósi J, Topál J: **What does it take to become 'best friends'? Evolutionary changes in canine social competence.** *Trends Cogn. Sci.* 2013, **17**:287-294.

10. Virányi Z, Range F: **On the way to a better understanding of dog domestication: aggression and cooperativeness in dogs and wolves.** In *The Social Dog: Behaviour and Cognition*. Edited by Kaminski J, Marshall-Pescini S. Amsterdam, The Netherlands: Academic Press; 2014:35-62.
- A good summary of the main dog domestication hypotheses.
11. Frantz F et al.: **Genomic and archaeological evidence suggest a dual origin of domestic dogs.** *Science* 2016, **352**:1228-1231.
12. Larson G, Fuller DQ: **The evolution of animal domestication.** • *Ann. Rev. Ecol. Evol. Syst.* 2014, **45**:115-136.
- A review of the different pathways to domestication (not just dogs).
13. Clutton-Brock J: *A Natural History of Domesticated Animals*. Cambridge, UK: Cambridge Univ Press; 1999.
14. Stahl PW: **Early dogs and endemic South American canids of the Spanish Main.** *J. Anthropol. Res.* 2013, **69**:515-533.
15. Coppinger R, Coppinger L: *What is a Dog?* The University of Chicago Press; 2016:2016.
16. Musiani M, Leonard JA, Cluff H, Gates CC, Mariani S et al.: **Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou.** *Mol. Ecol.* 2007, **16**:4149-4170.
17. Stronen AV, Navid EL, Quinn MS, Paquet PC, Bryan HM, Darimont CT: **Population genetic structure of gray wolves (*Canis lupus*) in a marine archipelago suggests island-mainland differentiation consistent with dietary niche.** *BMC Ecol.* 2014, **14**:11.
18. Lord K, Feinstein M, Smith B, Coppinger R: **Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*).** *Behav. Processes* 2013, **92**:131-142.
19. Hughes J, Macdonald DW: **A review of the interactions between free-roaming domestic dogs and wildlife.** *Biol. Conserv.* 2013, **157**:341-351 <http://dx.doi.org/10.1016/j.biocon.2012.07.005>.
20. Boyko AR et al.: **Complex population structure in African village dogs and its implications for inferring dog domestication history.** *Proc. Natl. Acad. Sci. U. S. A.* 2009, **106**:13903-13908 <http://dx.doi.org/10.1073/pnas.0902129106>.
21. Shannon LM et al.: **Genetic structure in village dogs reveals a Central Asian domestication origin.** *Proc. Natl. Acad. Sci. U. S. A.* 2015, **112**:13639-13644 <http://dx.doi.org/10.1073/pnas.1516215112>.
22. Pilot M et al.: **On the origin of mongrels: evolutionary history of free-breeding dogs in Eurasia.** *Proc. R. Soc. B* 2015, **282**:20152189.
23. Castroviejo-Fisher S, Skoglund P, Valadez R, Vila C, Leonard JA: **Vanishing native American dog lineages.** *BMC Evol. Biol.* 2011, **11**:73.
24. Pal SK: **Mating system of free-ranging dogs (*Canis familiaris*).** *Int. J. Zool.* 2011, **2011**:10 <http://dx.doi.org/10.1155/2011/314216> Article ID 314216.
25. Cafazzo S, Bonanni R, Valsecchi P, Natoli E: **Social variables affecting mate preferences, copulation and reproductive outcome in a pack of free-ranging dogs.** *PLoS One* 2014, **9**: e98594 <http://dx.doi.org/10.1371/journal.pone.0098594>.
26. Macdonald DW, Carr GM: **Variation in dog society: between resource dispersion and social flux.** In *The Domestic Dog: Its Evolution, Behaviour and Interactions with People*. Edited by Serpell J. Cambridge: Cambridge University Press; 1995:199-216.
27. Mech LD, Smith DW, MacNulty DR: *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey*. Chicago, IL: University of Chicago Press; 2015.
28. MacNulty DR, Tallian A, Stahler DR, Smith DW: **Influence of group size on the success of wolves hunting bison.** *PLoS One* 2014, **9**: e112884 <http://dx.doi.org/10.1371/journal.pone.0112884>.
29. Kaczensky P, Hayes RD, Promberger C: **Effect of raven *Corvus corax* scavenging on the kill rates of wolf *Canis lupus* packs.** *Wildl. Biol.* 2005, **11**:101-108 [http://dx.doi.org/10.2981/09096396\(2005\)11%5B101:EOCCS%5D2.0.CO;2](http://dx.doi.org/10.2981/09096396(2005)11%5B101:EOCCS%5D2.0.CO;2).
30. Cassidy KA, MacNulty DR, Stahler DR, Smith DW, Mech LD: **Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park.** *Behav. Ecol.* 2015, **26**:1352-1360.
31. Sen Majumder S, Pual M, Sau S, Bhadra A: **Denning habits of free-ranging dogs reveal preference for human proximity.** *Sci. Rep.* 2016, **6**:32014.
32. Paul M, Sen S, Sau S, Nandi AK, Bhadra A: **High early life mortality in free-ranging dogs is largely influenced by humans.** *Sci. Rep.* 2016, **6**:19641.
33. Atickem A, Bekele A, William SD: **Competition between domestic dogs and Ethiopian wolf (*Canis simensis*) in the Bale Mountains National Park, Ethiopia.** *Afr. J. Ecol.* 2009, **48**:401-407.
34. Vanak AT, Gompper ME: **Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition.** *Mamm. Rev.* 2009, **39**:265-283.
- Although focusing more on their impact as predators, this is the most complete review so far of the feeding habits of free-ranging dogs.
35. Silva-Rodríguez EA, Sieving KE: **Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate.** *Biol. Conserv.* 2012, **150**:103-110.
36. Ruiz-Izagirre E, van Woersem A, Eilers KCHAM, van Wieren SE, Bosch G, van der Zijpp AJ, de Boer IJM: **Roaming characteristics and feeding practices of village dogs scavenging sea-turtle nests.** *Anim. Conserv.* 2014:146-156.
37. Silva-Rodríguez EA, Sieving KE: **Influence of care of domestic carnivores on their predation on vertebrates.** *Conserv. Biol.* 2011, **25**:808-815.
38. Krauze-Gryz D, Gryz J: **Free-ranging domestic dogs (*Canis familiaris*) in Central Poland: density, penetration range and diet composition.** *Pol. J. Ecol.* 2014, **62**:183-193.
39. Axelsson E, Ratnakumar A, Arendt ML, Maqbool K, Webster MT, Perloski M: **The genomic signature of dog domestication reveals adaptation to a starch-rich diet.** *Nature* 2013, **495**:360-364 <http://dx.doi.org/10.1038/nature11837>.
40. Sen Majumder S, Bhadra A, Ghosh A, Mitra S, Bhattacharjee D, Chatterjee J, Nandi AK, Bhadra A: **To be or not to be social: foraging associations of free-ranging dogs in an urban ecosystem.** *Acta Ethol* 2014, **17**:1-8 <http://dx.doi.org/10.1007/s10211-013-0158-0>.
41. Sillero-Zubiri C, Gottelli D: **Diet and feeding behavior of Ethiopian wolves (*Canis simensis*).** *J. Mamm.* 1995, **76**:531-541.
42. Packard JM: **Wolf behavior: reproductive, social and intelligent.** In *Wolves: Behavior, Ecology, and Conservation*. Edited by Mech LD, Boitani L. Chicago, IL, and London: University of Chicago Press; 2003:35-65.
43. Lehman N, Oarkson P, Mech LD, Meier TJ, Wayne RK: **A study of the genetic relationships within and among wolf packs using DNA fingerprinting and mitochondrial DNA.** *Behav. Ecol. Sociobiol.* 1992, **30**:85-94.
44. Mech LD, Boitani L: **Wolf social ecology.** In *Wolves: Behavior, Ecology, and Conservation*. Edited by Mech LD, Boitani L. Chicago, IL: University of Chicago Press; 2003:1-35.
- A great summary of wolves' social behaviour and ecology.
45. Stahler DR, MacNulty DR, Wayne RK, vonHoldt B, Smith DW: **The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves.** *J. Anim. Ecol.* 2013, **82**:222-234.
46. Macdonald DW, Johnson DDP: **Patchwork planet: the resource dispersion hypothesis, society, and the ecology of life.** *J. Zool.* 2015, **295**:75-107.
47. Bonanni R, Cafazzo S: **The social organization of a population of free-ranging dogs in a suburban area of Rome: a reassessment of the effects of domestication on dogs' behaviour.** In *The Social Dog: Behaviour and Cognition*. Edited by Kaminski J, Marshall-Pescini S. Amsterdam, The Netherlands: Academic Press; 2014:65-104.

A comprehensive review of studies on the social behaviour of free-ranging dogs with more detailed results from a study population in Central Italy.

48. Pal SK: **Parental care in free-ranging dogs, *Canis familiaris***. *Appl. Anim. Behav. Sci.* 2005, **90**:31-47 <http://dx.doi.org/10.1016/j.applanim.2004>.
 49. Paul M, Sen Majumder S, Bhadra A: **Grandmotherly care: a case study in Indian free-ranging dogs**. *J Ethol* 2014, **32**:75-82 <http://dx.doi.org/10.1016/j.beproc.2013.10.006>.
 50. Paul M, Sen Majumder S, Bhadra A: **Selfish mothers? An empirical test of parent-offspring conflict over extended parental care**. *Behav. Process.* 2014, **103**:17-22 <http://dx.doi.org/10.1016/j.beproc.2013.10.006>.
 51. Boitani L: **Wolf management in intensively used areas of Italy**. In *Wolves of the World. Perspectives of Behaviour, Ecology, and Conservation*. Edited by Harrington FH, Paquet PC. Park Ridge: Noyes; 1982:158-172.
 52. Gipson PS: **Evaluations of behavior of feral dogs in interior Alaska, with control implications**. *Vertebrate Pest Control Manag Mater 4th Symp Am Soc Testing Mater* 1983, **4**:285-294.
 53. Tallents LA, Randall DA, Williams SD, Macdonald DW: **Territory quality determines social group composition in Ethiopian wolves *Canis simensis***. *J. Anim. Ecol.* 2012, **81**:24-35 <http://dx.doi.org/10.1111/j.1365-2656.2011.01911>.
 54. Dale R, Range F, Stott L, Kotrschal K, Marshall-Pescini S: **The influence of social relationship on food tolerance in wolves and dogs**. *Behav. Ecol. Sociobiol.* 2017. in press.
 55. Range F, Ritter C, Virányi Z: **Testing the myth: tolerant dogs and aggressive wolves**. *Proc. R. Soc. B* 2015, **282**:20150220 <http://dx.doi.org/10.1098/rspb.2015.0220>.
 56. Feddersen-Petersen D: *Hundepsychologie: Sozialverhalten und Wesen, Emotionen und Individualität*. Stuttgart: Kosmos Verlag; 2004.
 57. Feddersen-Petersen D: **The ontogeny of social play and agonistic behaviour in selected canid species**. *Bonner Zoologische Beiträge* 1991, **42**:97-114.
 58. Feddersen-Petersen D: **Social behaviour of dogs and related canids**. In *The Behavioural Biology of Dogs*. Edited by Jensen P. Trowbridge, UK: Cromwell Press; 2007:105-119.
 59. Range F, Virányi Z: **Wolves are better imitators of conspecifics than dogs**. *PLoS One* 2015, **9**:e86559 <http://dx.doi.org/10.1371/journal.pone.0086559>.
 60. Trut L, Oskina I, Kharlamova A: **Animal evolution during domestication: the domesticated fox as a model**. *Bioessays* 2009, **31**:349-360.
 61. Frank H, Frank MG: **Comparative manipulation test performance in 10-week-old wolves (*Canis lupus*) and Alaskan Malamutes (*Canis familiaris*)—a Piagetian interpretation**. *J. Comp. Psychol.* 1985, **99**:266-274.
 62. Hiestand LA: **Comparison of problem-solving and spatial orientation in the wolf (*Canis lupus*) and dog (*Canis familiaris*)**. *Behav. Genet.* 2011, **41**:840-857.
 63. Udell MAR: **When dogs look back: inhibition of independent problem-solving behaviour in domestic dogs (*Canis lupus familiaris*) compared with wolves (*Canis lupus*)**. *Biol. Lett.* 2015:0489.
 64. Marshall-Pescini S, Besserdich I, Kratz C, Range F: **Exploring differences in dogs' and wolves' preference for risk in a foraging task**. *Front. Psychol.* 2016, **7** <http://dx.doi.org/10.3389/fpsyg.2016.01241>.
 65. Mettke-Hofmann C: **Cognitive ecology: ecological factors, lifestyles, and cognition**. *Wiley Interdiscip. Rev. Cogn. Sci.* 2014, **5**:345-360.
- A fascinating review on the effects of ecology on a species' cognitive abilities.
66. Moretti L, Hentrup M, Kotrschal K, Range F: **The influence of relationships on neophobia and exploration in wolves and dogs**. *Anim. Behav.* 2015, **107**:159-173.
 67. Marshall-Pescini S, Virányi Z, Kubinyi E, Range F: **Motivational factors underlying problem solving: comparing wolf and dog puppies' explorative and neophobic behaviors at 5, 6 and 8 weeks of age**. *Front. Psychol.* 2017, **8**:180 <http://dx.doi.org/10.3389/fpsyg.2017.00180>.
 68. Scott JP, Marston M: **Critical periods affecting the development of normal and mal-adjustive social behavior of puppies**. *J. Genet. Psychol.* 1950, **77**:25-60.
 69. Klinghammer E, Goodmann PA: **Socialization and management of wolves in captivity**. In *Man and Wolf: Advances, Issues and Problems in Captive Wolf Research*. Edited by Frank H. Dordrecht: Dr. W. Junk Publishers; 1987:31-61.
 70. Range F, Virányi Z: **Social learning from humans or conspecifics: differences and similarities between wolves and dogs**. *Front. Psychol.* 2013, **4**:868 <http://dx.doi.org/10.3389/fpsyg.2013.00868>.
 71. Range F, Virányi Z: **Development of gaze following abilities in wolves (*Canis lupus*)**. *PLoS One* 2011, **6**(2):e16888 <http://dx.doi.org/10.1371/journal.pone.0016888>.
 72. Werhahn G, Virányi Z, Barrera G, Sommese A, Range F: **Wolves (*Canis lupus*) and dogs (*Canis familiaris*) differ in following human gaze into distant space but respond similar to their packmates' gaze**. *J. Comp. Psychol.* 2016 <http://dx.doi.org/10.1037/com0000036>. Advance online publication.
 73. Heberlein MTE, Turner DC, Range F, Virányi Z: **A comparison between wolves, *Canis lupus*, and dogs, *Canis familiaris*, in showing behaviour towards humans**. *Anim. Behav.* 2016, **122**:59-66 <http://dx.doi.org/10.1016/j.anbehav.2016.09.023>.