Cooperation and cognition in wild canids

Andreas Berghänel*, Martina Lazzaroni*, Giulia Cimarelli*,
Sarah Marshall-Pescini* and Friederike Range*

Canids are believed to be clever animals applying sophisticated social and hunting strategies. However, current studies under natural conditions do not indicate higher cognitive requirements beyond associative learning, but likely also underestimate them as applied methods are still in a fledgling stage. Experimental studies on captive canids — almost exclusively on wolves and dogs — indicate role understanding, perspective taking skills and numerical competence. However, such studies do not inform us if and how such skills are used in the wild. Apart from urging researchers to combine both approaches, we also highlight the need to investigate the embodied cognition of canids, as their specific ecological needs and perceptual capabilities likely led to specialised neuroethological pattern recognition skills.

Address
Domestication Lab, Konrad Lorenz Institute of Ethology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Savoyenstraße 1a, A-1160 Vienna, Austria

Corresponding Authors:
Andreas Berghänel (berghaenela@staff.vetmeduni.ac.at),
Martina Lazzaroni (Martina.Lazzaroni@vetmeduni.ac.at)
* Twitter account: @aberghaenel, @DomLabVienna, @CimarelliG,
@MarshallPescini, @FriederikeRange

Introduction

In tales all around the world, canids like foxes, wolves, jackals or coyotes often represent particularly intelligent individuals that trick their victims into traps with guile and cleverness. They are among the most cooperative mammals [1] and largest-brained carnivores [2]. Hence canids provide an important piece to the puzzle of cognitive evolution, and comparing them with other phylogenetically distant animals like feliforms, primates, cetaceans and birds will provide new insights into the convergent, independent

evolution of cooperation and cognition [3]. This applies in particular to comparisons with humans. Despite their phylogenetic distance, canids resemble humans more than other apes in terms of a) their cooperative breeding and monogamy and, consequently, low sexual size dimorphism [1,2], and b) their reliance on cooperative hunting that also targets large and dangerous prey [1,4–7], two aspects that were argued to be fundamental for the evolution of human-specific hyper-cooperation and cognition [1,2,4,8,9].

Indeed, the hunting strategies and social behaviour of many canids appear complex and often cooperative, and there is a widespread belief that this complexity and cooperativeness requires extraordinary, human-like cognitive abilities like foresight, planning and shared intentionality. Some studies support these beliefs, thereby proposing high cognitive capabilities in canids and other social carnivores (see for example, in [5,10,11]). On the other hand, several killjoy explanations arose that question the high cognitive requirements for such behaviour, arguing that simple innate or associatively learned heuristics may be sufficient [1,11], a demarcation line between higher and lower cognition that we will also apply in our review (see glossary). Such simple heuristics may particularly play out under natural, highly stochastic conditions, where rational inference may hardly yield better predictions and outcomes [12,13]. Indeed, the ecological relevance of experimental studies conducted in captivity has been questioned in general, leading to a rise in studies investigating cognition in the wild for a variety of species such as chimpanzees, dolphins, elephants, meerkats, hyenas and many other vertebrates and invertebrates [3,14]. This provides animals with the natural experiences, tasks, settings and complexities under which cognitive skills evolved and can naturally develop and play out, including the advantages of evolved neuroethological solutions and rules of thumb [13–16].

Here we provide a critical review of the occurrence of higher cognition in canids, particularly in relation to cooperation, drawing both from studies in the natural context and in the lab. We discuss their relevance under natural conditions and whether alternative, lower-level explanations may suffice to explain findings. To achieve these aims we will address canid cognition from two directions: we will first critically scan natural canid-typical behaviour for the necessity of higher cognitive skills (Figure 1, Table 1) and then critically examine

Figure 1
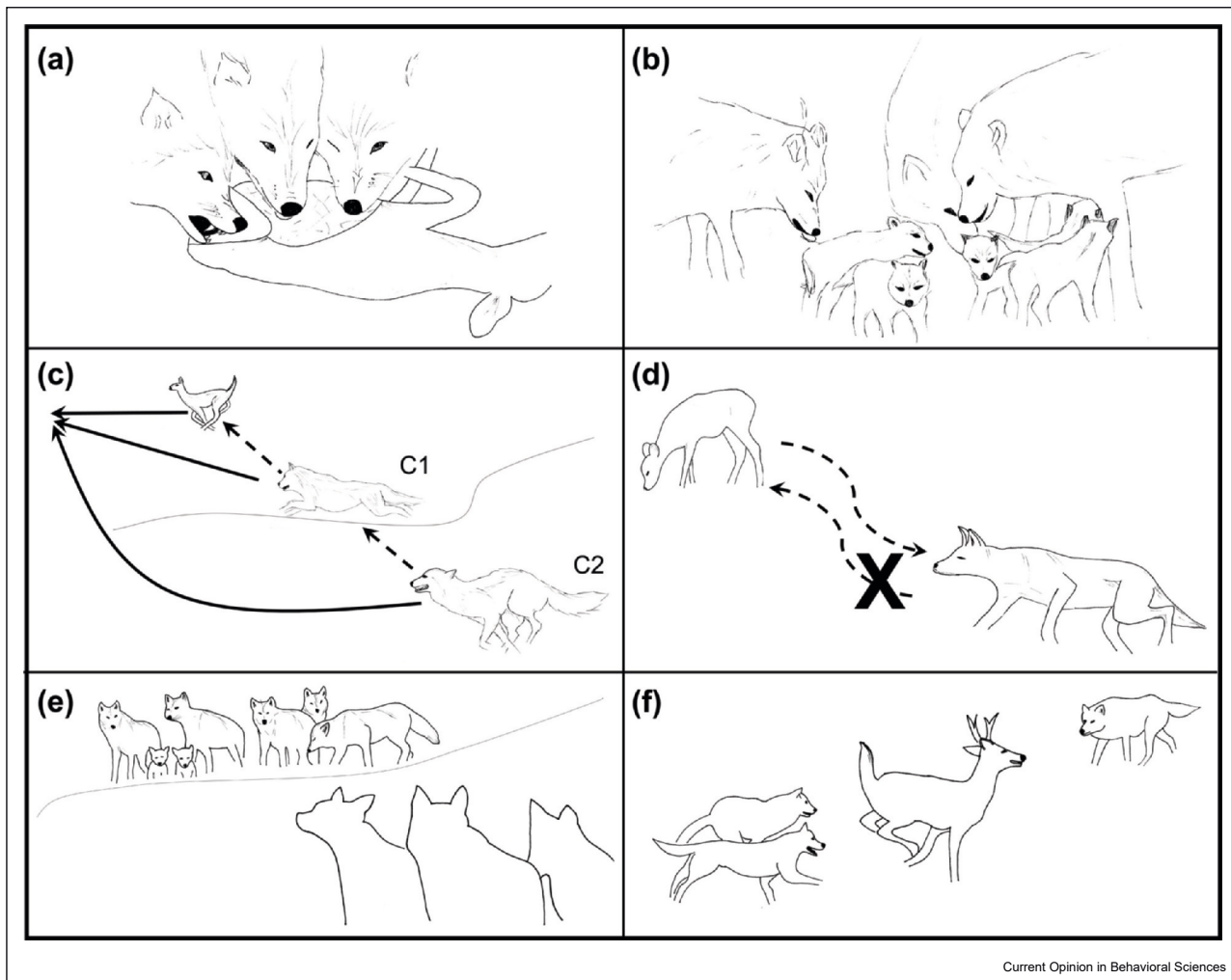
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The different natural settings in which higher cognition beyond associative learning could be required or helpful in canids. **(a)** Social tolerance means sharing of resources by dominant individuals although they could monopolise them. Generally, this requires inhibitory control, but in species with high average relatedness it might also evolve as a fixed behaviour towards group members in general (Box 1). **(b)** Cooperative breeding means that non-parents also take care of or even feed puppies. It might not require higher cognition but benefits from prosocial behaviour, which can also evolve as a fixed behavioural trait. **(c)** When chasing prey or competitors, it is more efficient to run towards the anticipated intersection point instead of the current position of the target. C1: For a direct setting (target visible), this ability requires no cognitive abilities (some insects excel on it and require only a few specified neurons). C2: The indirect setting (target not visible but conspecific cues available) would require successful social cue reading, and it remains interesting whether this occurs in canids and whether it could be automatised similar to, for example, primate face recognition. **(d)** Ability to take the perspective and sensory skills of the target into account (here: staying upwind). This remains an outstanding research question, with current evidence allowing for simple innate explanations. **(e)** Assessment of fighting power relationships during encounters with prey, competitors, and conspecifics. Can be based on differences in numerosity (like quantity or mass, widespread skill across animals) and/or more complex aspects like group composition and cohesion. Could be based on automatized pattern recognition and fast heuristics, especially since fast decision can be crucial. **(f)** Collective hunting and encounters with allo- and conspecific competitors. Collaborative hunting is typically assumed to require coordination of individual roles, but complex pattern could also emerge from simple rules of thumb, synchronisation, and/or self-organisation processes, and real interaction dynamics are difficult to quantify in the wild. In case of similar roles (here the two chasers), it is difficult to obtain from observations alone whether active coordination is involved. It might be more obvious in case of complementary roles (here ambusher and chaser), but also here, many observed patterns could emerge from associative learning, innate rules of thumb, physical differences that predestine for certain roles, or just be coincidences. However, there is experimental evidence from captive wolves and dogs for the capability to consider a partner`s role and probably also it`s perspective and intention, which could allow for complex hunting strategies.

evidence from the lab for a variety of cognitive skills and evaluate how they may be relevant in the wild (Table 1). Since canid cognition remains heavily understudied, with most studies conducted with captive wolves and dogs, we will refer to non-canid species like hyenas, lions or primates where needed for comprehensiveness, and in particular to show potential future avenues for canid research. Finally, in Box 1, we will further discuss how

Table 1

Tasks under natural conditions and potentially associated cognitive abilities, and evidence from experimental studies in Canids.

Function/task	Cognitive skill	Killjoy explanation	Evidence for cognitive capability in canids	References
Assessment of strength of own group and opponent (conspecifics/thieves/prey)	Quantity discrimination (Numerosity)	Widespread in animals including invertebrates, minimal neural requirements	Between-group encounters decided by group size (wild wolves, free-ranging dogs). Quantity discrimination observed in captive wolves, dogs and coyotes	[32,33,39–41]
	Assessment of group composition, cohesion and resource ownership	Simple innate heuristics and pattern recognition might be sufficient (e.g. group spread or movement synchrony)	Between-group encounters also decided by proportion of adult males (wolves) and species difference in power, presence of adult males and ownership (lions vs hyenas)	[32,39,41,44]
Hunting and intergroup conflicts	Heading-off	Widespread in animals including invertebrates Minimal neural requirements	Anticipatory looking and motion tracking in dogs	[11,35]
	Gaze following	Motion following reinforced via operant conditioning Innate detection of others' gaze direction and behavioural correlates of attention	Gaze following behaviour observed in both dogs and wolves, also into far distance and behind barriers	[73–75]
	Perspective taking*	Some pattern explainable by simple behavioural rules, innate processes or associative learning	Perspective taking in both wolves and dogs	[82,84–86]
Detect & avoid cheating, facilitate cooperative action	Inequity aversion	Mere inequity detection: Recognising difference in outcomes or violation of expectations (operant conditioning) sufficient, probably widespread across vertebrates. Emotional mediation.	Wolves and dogs refuse to participate when receiving an inequity treatment compared to the social partner	[60]
	Bookkeeping of reciprocity	Emotional mediation	Short-term direct reciprocity in dogs	[63,66]
Coordination during collective action	Synchronisation	Simple rules of thumb sufficient (simulations) Evident also in fish, reptiles and invertebrates	Synchronisation between dogs and humans Synchronous action in cooperative task (wolves)	[10,11,46,51,71,78]
	Inhibitory and self-control	Mediated by social relations/emotions	Success in delayed gratification task (wolves) Cofeeding at monopolizable food patch (wolves)	[67–72]
Collaboration	Taking roles	Physical constraints Social or associative learning Evident also in fish (innate species-specific roles)	Wolves choose to act at the same apparatus at the same time (coordination in space and time)	[10,11,71]
	Understanding other's roles*	/	Wolves and dogs wait for and recruit partners	[10,11,71]
	Understanding other's intentionality*	/	Dogs recognise humans' intention-in-action	[83]

* Potential higher cognitive skill.

Box 1 Socioecology, social tolerance, and the applicability of cooperation and cognitive skills.

Socioecological conditions can facilitate or constrain cooperation and thus the detectability of associated cognitive skills in captivity and in the wild. This is obvious in solitary species due to limited social opportunities, but applies also to gregarious species. Hence variation within and between natural and captive settings in, for example, food characteristics and group composition may influence the detectability of certain cognitive skills.

Social tolerance: license to share
Cooperation typically requires sufficient benefits for all participants which may come through sharing in the obtained resources (Figure 1a). Sharing of resources is straightforward if a resource is not monopolizable, and large carcasses allow for peaceful cofeeding and cooperative hunting even between otherwise solitary carnivores [95,96]. However, sharing becomes problematic if the resources can be monopolised by certain individual(s). Under such conditions, social tolerance becomes a prerequisite for the occurrence and maintenance of cooperative interactions [31,71,79,80,97] as it facilitates sharing of benefits and reduces mutual avoidance.

Social tolerance between kin and non-kin
Social tolerance is easiest facilitated between close kin, where benefits of one partner automatically translate into benefits of the other, thereby reducing the benefits of monopolisation and the importance of equal share and inequity aversion [24]. Due to their family structure and high reproductive skew, most gregarious canids likely have high average relatedness between group members [2]. In such species, social tolerance could evolve as a fixed motivational trait that applies to all group members irrespective of actual relatedness, which would further ease the evolution of generalised cooperation, generalised reciprocity, and prosociality [2,9,24].

Social tolerance can also occur between unrelated individuals if dominants depend on subordinates for, for example, cooperative hunting or defence ('subordinate leverage', [80]). This should lead to concessions by dominant individuals in terms of resource sharing to maintain cooperation, and dominants will benefit from the ability to inhibit their monopolisation potential to facilitate sharing [80]. Accordingly, social tolerance is related to enhanced inhibitory control in macaques [97], and inhibitory control was also shown for wolves and dogs, at least if properly trained (see main text).

Social tolerance and cooperation in canids
Only few studies on captive and wild canids explicitly showed their high social tolerance [26,68,89,98], though numerous case reports exist. Studies conducted in captivity provided direct evidence for the link between social tolerance and cooperation. Wolves typically live in family groups encompassing one breeding pair and their offspring, and benefit from cooperative hunting, breeding and carcass defence, whereas dogs seem to do neither [30,68]. This difference is reflected in their level of social tolerance, with wolves but not dogs being tolerant around a food source [30,68,99]. Consequently, wolves outperform dogs in a conspecific cooperation task, and this difference was apparently due to cofeeding tolerance in wolves and mutual avoidance in dogs [71]. To what degree these differences might relate to differences in relatedness remains however unknown.

Pair-living monogamy → Kinship → Social tolerance → Cooperation Prosociality → Inter-dependency

In canids, monogamy and kinship may lead to social tolerance, which facilitates cooperation in hunting, pup rearing and resource defence. The resulting interdependency further strengthens the need for social tolerance.

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socioecological conditions can facilitate or constrain cooperation and the exhibition of cognitive skills (Figure 1a).

Canid cognition: evidence from the wild
Cooperative breeding
Cooperative breeding with alloparental care occurs when individuals other than the breeding pair help to raise offspring, either passively via babysitting and protection or actively by food provisioning, allonursing, transport, hygienic care and adoption (Figure 1b; [9,17]). Cooperative breeding is widespread in canids and ranges from facultative (helpers not necessary but beneficial, for example, wolves [18]) to obligate (helpers required to successfully raise any offspring, for example, African wild dogs [19]). The typical canid social system is one monogamous breeding pair raising their pups, often with

the help of older offspring who thereby gain indirect fitness benefits through kin selection, which might become increasingly important under habitat saturation [2,20]. However, sometimes also non-kin immigrants join the group and help to raise the offspring, probably for the benefits of group membership and potential territory inheritance [2,21].

Cooperative breeding does not require but may benefit from higher cognitive skills
Cooperative breeding does not require higher cognitive skills as changes in motivation towards delayed or skipped dispersal and prosocial caregiving might be sufficient [22]. Proactive prosociality increases with increasing allomaternal care in primates and corvids [8,23]. In species with high average relatedness within groups due to, for example, high reproductive skew which is

typical for canids, such motivational settings can be evolutionary selected for as fixed or developmentally plastic traits [9]. Indeed, in contrast to other species, cooperative breeders show more generalised cooperative behaviour, which is not affected by the actual relatedness between interactors ([24]; see also Box 1). The underlying motivational setting can mechanistically be achieved by hormonal changes, such as reduced testosterone and glucocorticoid levels, and increased levels of prolactin and oxytocin which are both involved in maternal caregiving and lactation and may simulate paternity and initiate caregiving tendencies [17,25]. This is particularly prominent in canids, where all species show obligatory pseudopregnancies which can trigger lactation and facilitate allonursing (see glossary; [2,25]). In combination with the ability for regurgitation in all canids [2] and a tendency to give pups and yearlings priority of access to carcasses in African wild dogs and possibly also wolves and dholes [26], this highlights the relevance of cooperative breeding in this genus [2], but also how complex behavioural adaptations relating to cooperation can be achieved by natural selection without the need for higher cognitive abilities. Nonetheless, even though higher cognitive skills may not be required for cooperative breeding to evolve, they can still provide benefits. For example, dependent offspring may benefit from intention reading skills to detect positive and negative attitudes in others, and from enhanced communication skills [9].

Cooperative breeding can facilitate cooperation and higher cognitive skills

Cooperative breeding may facilitate the evolution of higher cognitive skills in two ways. First, it can increase the level and reliability of available resources during development, which may allow for the evolution of enlarged or more complex brain structures ([27], but see [28,29] for a comprehensive critique on measures and cognitive correlates of brain size). Second, the higher levels of social tolerance and prosociality associated with cooperative breeding may set the ground for other and more complex forms of cooperation that then also require and/or benefit from higher cognitive skills ([9]; Box 1]. Studies on wolves highlighted their prosocial motivations in helping adult conspecific partners beyond cooperative breeding [30]. Such general prosocial motivation predicts social coordination and cooperative problem solving in primates [9,31], but no study has investigated this correlation in canids.

Cognition and cooperation during hunting and resource defence

Hunting and defence against conspecific and allospecific competitors can involve single individuals or groups, depending on species and circumstances. Cooperative hunting enables capturing of more dangerous prey [6], and cooperative carcass defence against other species like hyenas for African wild dogs or ravens for wolves

influences net energy intake [7,30]. Similarly, cooperative defence against other conspecific groups can be crucial since such encounters can be lethal and influence territory quality and size [2,30]. Hunting and defence against competitors involve similar battle strategies and may benefit from a) fast estimation of shortest paths and path intersection when attacking and when being attacked (Figure 1c), b) consideration of the perspective and knowledge of the counterpart (Figure 1d), c) reliable assessment of fighting power (Figure 1e), and d) enhanced coordination during cooperative action (Figure 1f; [1,10,11,32–35]). Therefore, we will examine hunting and other encounters together, focusing on one or the other depending on its relevance and amount of evidence.

Path estimation and intersection: does heading-off imply foresight?

Heading-off a target by cutting edges requires interpolation of escape path (Figure 1c). This skill is widespread in canids, though it was explicitly shown only for dogs [34]. However, it is also evident in fish [34], and even in invertebrate species like dragon- and damselflies that are extraordinarily skilled in fast and dynamic intersection estimation with high capture success [35]. In invertebrates, such computations can be hard-wired and provided by only a handful of neurons which directly link visual input to flight motor neurons [35]. To what degree individuals may further use social information from co-hunters like ear, gaze and body orientation to estimate the position and movement-vector of prey that is not visible for them requires further research [11].

Staying upwind: does it imply perspective-taking?

Strategic hunting against the wind to avoid detection by prey during ambushing or stalking was thought to require high cognitive abilities like perspective taking (Figure 1d), but such behaviours seem rare or absent in carnivores. Lions do not consider wind direction when stalking prey [36]. Wolves sometimes rest next to predictable animal-ranging sites for many hours, positioning themselves such that the wind comes from where the prey could emerge [37]. However, although interpreted as strategic avoidance of detection by prey [37], a more parsimonious explanation might be that wolves position themselves such that they have an optimal olfactory and acoustic view and can detect prey without being permanently visually alert [38]. For olfactory species this might be as basic as positioning themselves to have an unobstructed view for visual animals like humans. Indeed, wolves may simply rest where the coming air smells most like prey habitat.

Assessment of fighting power: numerosity and beyond

The ability to assess one's own and other's strength to decide between attack or retreat is similarly important during hunting and encounters with conspecifics or allospecific competitors like ravens or hyenas (Figure 1e). During intergroup encounters, a wide range of vertebrate

and invertebrate species including wolves and dogs are able to compare numerosities and adjust their fight-or-flight propensity accordingly, and this is probably provided by simple innate mechanisms of perceptual pattern recognition [32,33,39–41]. In birds and mammals including humans and dogs, numerosity-selective neurons that generalise over different physical appearances (rearrangements of dots or items, temporal sequences, hand movements) and even different modalities (visual and auditory) have been detected [42]. However, in birds and mammals, estimation accuracy increases with cortical neuron density and a score of general cognitive ability [43].

Animals may also consider other, more complex aspects like individual strength, group composition, social cohesiveness, and resource ownership during such situations (Figure 1e; [32,41]). For instance, during intergroup encounters, wolves take the proportion of adult males into account [39], and encounters between lions and hyenas over food patches are decided by a range of criteria including number, species difference in individual power, presence of adult male lions, and resource ownership [44,100]. Similar assessment processes may also act during hunting, and help decide whether to attack a group of bison or wildebeest depending on the size and cohesion of the own (hunting) and the prey group [5,6]. Wolves, for example, typically aim to flush their prey, and can wait for hours until their prey starts to move before they attack, which might also allow them to better assess their prey [5,11]. During both hunting and intergroup encounters, wolves aim to separate and then attack single and potentially weak individuals, thereby changing power asymmetry to their advantage [5,45].

It remains unclear how such more complex assessments during hunting or other encounters would require or benefit from higher cognition beyond mere pattern recognition and associative learning, and to our knowledge there are no studies that address this question directly. A priori, the involvement of higher cognition would probably not be necessary and often also not be helpful. In complex situations that require fast decision, also humans tend to rely on simple heuristics which often provide equal or even more accurate prediction [13]. Simple patterns like average distance between individuals, group spread, or movement synchrony may provide sufficient information [13].

Cooperation: acting together
Wolves spreading out, encircling, and separating their prey look impressive and coordinated, and similar tactics can be observed during intergroup encounters (Figure 1f; [1,5,11,45]). However, Muro et al. [46] have shown that similar behaviour can be generated in simulations based on two simple behavioural rules (getting the closest safe distance to and the best view on the prey), and many other simulations suggest that a wide range of different strategies in reaction to prey characteristics and hunting group size can be achieved by simple rules of thumb (e.g. [47,48]). Indeed, coordination could result as a simple cognitive mechanism that does not require communication or monitoring of the partners [49] but is driven by behavioural synchronisation of the subjects or just by-product mutualism emerging from multiple selfish agents acting in parallel [50], which were argued can sufficiently explain most group hunting in carnivores and also chimpanzees [4,10,11]. This interpretation may be supported by recent findings of coordinated predation in cold-blooded vertebrates like electric eels that cooperatively encircle fish and launch synchronous predatory high-voltage strikes through the shoal [51] which further suggests that the evolution of such behaviour may not require higher cognition.

Collaboration and coordination
Individuals may collaborate with each other beyond mere synchronisation when adopting similar or complementary roles (Figure 1f; [10,11]). Coordination of similar roles occurs when, for example, two individuals approach a target from different sides in a similar, but actively coordinated way. Such behaviour seems frequent in social canids but may often build on simple rules of thumb, such as keeping the target at a straight line between two or the centroid between multiple actors (e.g. lions: [52]). Indeed, also the above-mentioned eels communicate during hunting, and it is difficult to conclude from observation alone whether such behaviour involves active coordination or is simply based on innate triggers.

Complementary roles seem unnoticeable during intergroup encounters or resource defence in canids but may occur during hunting with, chasers encircling and then chasing the prey in the direction of ambushers, for example (Figure 1f; [10,11]). Such task differentiation during hunting was first observed in wild lions and chimpanzees but has been reported — anecdotally — to occur also in canids like wolves, coyotes, golden jackals or bush dogs [5,10,11,52]. It remains an open question though to what extend these occasions represent collaboration or mere coincidental constellations, where, for example, prey accidently runs into wolves that had just fallen behind or coincidently rest at a trail [5]. In lions and chimpanzees, stable individual preferences for certain roles were found [4,52], which could however be the consequence of physical differences [5,10], with, for example, slower and stronger individuals taking ambusher and lighter but faster individuals taking chaser roles [11], which also plays a crucial role in hunting role differentiation in human hunter-gatherers [4]. Predators may also tend to start chasing if the prey moves away and to ambush if the prey is heading towards them [52]. Moreover, it was argued that such collaboration could be based on associative learning [10,11]. Collaborative hunting relationships occur even between fish species

taking different, evolutionary fixed hunting roles, with cooperative action involving recruitment behaviour and probably referential gestures [10,53]. This raises the question to what degree such role differentiation might become fixed also within species, either genetically or through development [10]. Hence, complex collaborative action may not necessarily require elaborated cognition, and it is difficult to derive from natural observations whether individuals understand the own and other's role [10,11].

Collective action problems: do canids cheat?
Group hunting and defense provide a perfect ground for collective action problems where individuals can gain benefits without paying the costs of participating. During intergroup encounters (dogs) and cooperative hunting (wolves), free-ranging dogs and wild wolves adjust their investment to the current requirements, which can result in free-riders [54,55]. Individuals reduce their effort and participation with increasing numbers of cooperation partners, particularly when the own pack has a numerical advantage over opponents (dogs, [54]), or when hunting group size reaches some threshold which is higher in case of larger and more formidable prey [wolves hunting elk or bison [6,55]). Dog participation further increases with increasing social integration, and wolves' hunting effort was higher in breeding than non-breeding individuals, hence motivation could be related to kin selection and reflect cooperative breeding prosociality [26,54,55,100]. Taken together, these findings may indicate collective action problems, but it remains unknown whether free-riding actually reduces success and individual net gain or represents only an adjustment of group effort.

Canid cognition: evidence from experimental settings
Altogether, there seems to be no strong evidence for the necessity of higher cognitive abilities during hunting and other (inter-)actions in canids [1,5,11]. However, current research on wild animals may underestimate the cognitive requirements for a certain behaviour. Complex and highly variable interactions like group hunting and defence are still difficult to quantify in sufficient detail, and it remains often unclear to which degree the observed pattern could emerge from stochastic and self-organising effects. Do wolves, for example, apply a coordinated hunting strategy or do they simply and patiently keep dynamics alive until a certain spatial pattern emerges (the segregation of a single prey from the group) that then triggers a collective attack - simply shaking the system until something falls out? Furthermore, since cooperation does not require advanced cognition *per se* [10], cognitive complexity can generally not be inferred from observing cooperation but must be demonstrated experimentally [49]. Additionally, even if they may not be necessary, many cognitive skills may still have

evolved and be used in the wild simply because they bring more benefits than costs [11].

In this section, we will therefore summarise results from experimental studies, which in canids were so far largely conducted on captive animals, and almost exclusively on wolves and dogs. Such studies allow the breakdown of complex natural constellations into separate, operationalizable aspects and can create artificial challenges where otherwise unnecessary cognitive skills become necessary and thus visible. Hence, they are particularly suited to provide proof of principle for cognitive abilities which would be difficult to obtain under ecological conditions, even though they do not necessarily show natural behaviour or the context in which a certain skill may be used in the wild [3,14,15].

Associative and social learning
Most canid species are generalists, and some like red foxes and wolves have adapted to a wide range of ecosystems across the globe and show fast individual adaptation to anthropogenic environments [2]. Not surprisingly then, they also show notable learning skills during experiments [30]. Wolves, dogs and coyotes were also able to learn from conspecifics [56], and such social learning could enhance adaptation to new environments and also favour the spread and coordination of cooperative behaviour in general [57,58]. However, no study has directly investigated the effect of social learning on cooperation in canids. In any case, the current evidence suggests a high potential of learning in canids, and the cognitive flexibility and learning abilities of canids deserve much more research.

Inequity aversion and reciprocity tracking
The maintenance of cooperative hunting and resource defence typically requires sufficient benefits for all participants and detection of free-riders. The detection and avoidance of inadequate benefit distribution can be facilitated by inequity aversion and tracking of reciprocal exchange [59,60]. Inequity aversion (the resistance to inequitable outcome) helps to detect and avoid inequity and exploitation between cooperating individuals, and to reconsider cooperation [59]. Inequity aversion has been extensively demonstrated in dogs, which are among the best studied species in this field [60]. However, in these experiments, inequity aversion was never investigated in a cooperation context, impeding direct translation of these findings to the relevant natural context. Nonetheless, after experiencing unequal treatment, pet dogs avoided each other [60], suggesting that inequity treatment might indeed reduce social tolerance, possibly affecting future cooperation propensity (Box 1).

Benefits might be balanced across multiple interactions, involving long-term reciprocal exchange of different commodities like cofeeding tolerance and participation in cooperative hunting and defence, which makes it difficult to

investigate reciprocity in natural settings [61]. Among Canids, only few experimental studies investigated reciprocity in dogs, showing evidence for short-term direct and also generalised reciprocity [62,63], which would match the above-mentioned potential challenges during collective actions. Captive dogs and wolves memorise the behaviour of human experimenters acting either selfish or generous [64,65] and subsequently prefer to approach the more generous experimenter, which they do independent of their social bond strength with the actors [65]. Such differentiation skills would likely pay during dangerous hunting where partner reliability and trustworthiness are vital. However, tracking of reciprocity and inequitable outcomes might not be cognitively demanding if they can be achieved through emotional mediation [66].

Inhibitory control

In order to cooperate, individuals might need to refrain from exhibiting prepotent and disadvantageous actions. Collaborative hunting events will likely fail if either individual ambushers or chasers act before all individuals are in position (Figure 1f; [11]). Moreover, inhibitory control can play a role in the maintenance of social tolerance (Box 1, Figure 1a). Inhibitory control has been investigated in wolves, dogs and coyotes [67,68], and studies conducted on dogs found a positive correlation between inhibitory control ability and problem-solving success [69,70]. The role of inhibitory control on cooperation was shown in the delayed loose-string paradigm where successful wolves and dogs waited for their partner to arrive, inhibiting themselves from pulling the rope [71]. Additionally, wolves and dogs have been tested in self-control, which is the ability to delay an immediate benefit pursuing a future more advantageous outcome [72]. Both wolves and dogs show inhibitory control abilities in delay of gratification tasks, with dogs performing generally better than wolves [68]. However, while they performed rather well in some studies especially if a human was present and/or some training was incorporated in the task, without these two aspects, also the majority of pet dogs basically failed [68].

Coordination

Cooperative interactions during hunting or group encounters may often benefit from successful coordination between partners [50]. Evidence for complex forms of coordination in canids has been observed in wolves and dogs. They can join their attention with humans and follow their gaze behind barriers, and both species can follow conspecifics gaze into distant space [73–75]. This ability could allow partners to use the others' gaze cues to enhance their coordination in space and time, including indirect tracking of prey through social cues (Figure 1 C2). Studies showed that wolves and dogs successfully coordinate both in space and time in a problem-solving task mimicking a hunting situation [76] as well as in a loose-string task where also hyenas and lions succeeded, potentially highlighting the importance of such skills in group-

hunting predators [10,71,77–80], although such skills are not limited to group hunters but were also shown for other species like ravens [81]. Importantly, if provided with multiple identical string-pulling apparatuses, wolves were able to coordinate their action to sequentially solve the task [71]. However, so far these tests do not allow to differentiate whether these coordination abilities reflect associative learning (i.e. conditioning) or involve higher cognition like perspective taking or causal reasoning [10].

Collaboration: considering the role and representing the perspective of others

Collaborative interactions could benefit from understanding and considering one's own and the partner's functional role, relevant also for wolves and dogs [10]. Wolves were shown to wait for their partner's arrival before acting in the string-pulling task [71], but mixed results emerged for dogs [71,77]. Both species were additionally able to recruit a human partner and did so only when the latter was needed to solve the task [78].

Collaborators may not only understand the functional role but also the perspective and intention of their partners. Shared intentionality and joint action would involve the representation of the other's perspectives and mental state [82]. Studies on dogs have shown their ability to understand human intentional and unintentional actions [83], to distinguish between different human attitudes [84] and to take another's perspective [85]. Interestingly, a recent study has found that instead of choosing randomly between two humans offering a toy, dogs re-engaged the specific human partner with whom the play session was suddenly interrupted. Such behaviour has been considered one marker of joint intentionality [86].

Conclusions

Overall, experimental studies on canids provide evidence for some skills that could be used for cooperation and other tasks in nature [10,49]. However, apart from showing that wolves and dogs can consider their partners' role and perspective, none of the studies explicitly tested or demonstrated higher forms of cognition, in that most results could potentially be explained by innate heuristics or associative learning. This is particularly important since typically, study animals have extensive experience with the testing situation, and the tests often involve many trials, which is often demonstrated by analyses showing learning effects [10,71]. Additionally, experimental studies have been conducted primarily on wolves and domestic dogs and to some degree coyotes, which does not allow for generalisations across canids as yet.

Showing a certain cognitive capability under experimental challenges does not necessarily mean that it is also typically exhibited when facing the day-to-day challenges in nature. It may instead be just a last resort to deal with special circumstances where simpler heuristics may not be available or

fail [11,15,33,87]. Indeed, the role of simple heuristics in humans is assumed to facilitate faster and more efficient responses and decisions, making them particularly efficient under complex routine situations and high uncertainty [12,13]. When given the choice, wolves and dogs rely on non-numerical cues to discriminate quantities, although at least wolves also have a mental representation of small quantities [88]. Wolves often follow a trial-and-error strategy during hunting [5], and African wild dogs prefer habitats where messy trial-and-error hunting is sufficient, and use elaborated tactics only under unfavourable conditions [89]. The actual socioecological conditions may further favour or constrain the application of specific skills (Box 1; [71,90]).

For ethical and other reasons, experimental settings largely reflect play contexts and do not mirror existential needs. Thus, on the one hand, the relative unimportance of the outcome may result in an underestimation of higher cognitive skills, while on the other hand, the reduced time pressure, low environmental complexity and high predictability could allow for thorough and accurate rational assessment, facilitating the application (and visibility) of higher cognitive skills [12–15].

Therefore, it is crucial to not only ensure reliable detection of cognitive skills in experimental settings but also to investigate the actual use of such cognitive abilities under natural conditions to estimate their biological significance, or in the best case to combine both approaches [14,15]. Tests in captivity would benefit from the consideration of socioecological covariates like dominance, age and sex relationships (Box 1) and from more realistic complexities. Such complexities may include multiple individuals allowing for free communication, partner choice, competition, role switching and complete behavioural sequences, as well as generally engendering a greater degree of unpredictability [14,50]. Experiments under natural conditions may hugely benefit from the steady advance in statistical methods and remote sensing, including combinations like playback and other devices triggered by camera traps with species recognition, plus data from, for example, GPS devices, proximity detectors, accelerometers or auto-tracking camera drones [14,91]. Observational studies in natural settings may utilise natural behaviour like recruitment behaviour during cooperative interactions, and natural contrasts like seasonal changes (e.g. [14,15,92]). The generalist ecology and high adaptability of many canid species to new, anthropogenic environments may provide a unique opportunity to investigate their cognitive flexibility in semi-natural settings, since reliance on innate and to some degree also individually learned heuristics would lead to predictable evolutionary traps. The main challenge may be to consider differences in previous experience and associated neophobia effects [15].

Outstanding questions

Apart from the urgent need of research on many more canid species before they or their natural habitats disappear [15], it would be particularly important to investigate canid learning abilities (how fast can they learn and how flexible are they once they have learned a certain response) as well as the role of socioecological aspects like kinship. Additionally, agent-based models could not only deepen our understanding of the minimal requirements for successful canid behaviour also under realistic conditions [46,93], but also the potential costs and benefits of additional cognitive skills. Here, a review of the many 'grey wolf optimiser' and similar simulations for industrial purposes (e.g. [47,48]) may bring new insights.

Lastly, it would be important to understand and consider the specialised perceptual landscape of canids and the potential for, for example, complex olfactory pattern recognition (innate or acquired), similar to, for example, face recognition in visual animals like primates. We also need a better understanding of the innate canid- or predator-specific neural abilities to automatically detect complex patterns within their relevant environment and ecological specialisation (as shown for many predator species like raptors, spiders and dragon flies, [16,35,94]), in particular because some may be absent in humans and thus would be misinterpreted as higher cognitive skills from an anthropocentric perspective (e.g. [29,90]).

Author contributions

A.B. and M.L. contributed equally. A.B., M.L. and F.R. conceptualized the manuscript and A.B. and M.L. wrote the manuscript, with all other authors providing critical additions and revisions during conceptualization and writing. G.C. drew the figures. All authors approved the final version of the manuscript for submission.

Conflict of interest statement

None.

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Glossary

Heuristics: Here defined as innate or learned rules of thumb that allow for fast and sufficiently accurate assessment of certain situations. Heuristics probably play an important role in animal and human decision making, especially under time pressure and complex or uncertain conditions. The danger of estimation error in critical situations like encounters can be buffered through decision bias towards the safer option, which in turn may be modified by motivational states that reflect, for example, energy balance or resource value 13.

Higher cognition: This term is not consistently defined. Here we define it through behaviourist exclusion as all cognitive processes that involves flexibility beyond mere stimulus-response associations and thus cannot be parsimoniously explained by associative learning (classical and operant conditioning), innate heuristics, or hard-wired neural circuits. Typically, this encompasses flexible processing and response to sensory information, including reasoning, creativity, rational decision making, planning, problem-solving and understanding.

Inequity aversion: Resistance to inequitable outcomes

Reciprocity: Reciprocity occurs when two or more social partners help each other in turn. General reciprocity implies that individuals help others if they received help from someone else, while direct reciprocity refers to the exchange between the same partners. Direct reciprocity might require individuals to memorise previous interactions (calculated reciprocity) or might be triggered by emotional states either short-term based on the partner's previous attitude ('attitudinal reciprocity') or long-term through the formation of social bonds ['emotional bookkeeping', 66,92].

Self-control: The ability or capacity to obtain a subjectively more valuable outcome rather than a subjectively less valuable outcome through choosing and then tolerating a longer delay or a greater effort requirement for obtaining that more valuable outcome [67]. It is a form of behavioural inhibition which not only implies suppressing impulsive reactions, but also decide as to whether a delayed gain is worth waiting for.

Gaze following: The ability to align one's own gaze with others to focus on external objects.

Joint attention: The ability to coordinate one's attention with another to an external object.

Cooperative loose string-pulling task: A widely used cooperative task where two individuals simultaneously pull on two rope ends to move a baited tray within reach to obtain the reward. The task fails if only one subject pulls one end of the rope. [71]

Collective behaviour: Miscellaneous set of behaviours by large numbers of individuals acting with or being influenced by other individuals.

Cooperative behaviour: Interactions that on average result in net gain for all participants. It includes reciprocity, mutualism and collective action [50].

Synchrony, coordination and collaboration: Cooperation can involve different levels of increasing cognitive complexity: similarity (similar actions with no relation in space and time), synchrony (similar actions related in time), coordination (similar actions related in space and time) and collaboration (different but complementary actions to achieve a common goal) [11].

Social tolerance: This term is used differently across fields specifically in psychology and behavioural ecology. Here we use the more narrow, socioecological meaning that an individual shows tolerance towards others and shares a resource although it could do differently, i.e. it does not insist on its existing monopolisation potential.

Prosocial behaviour: Behaviour that results in a benefit for others at no costs to the actor (altruistic when costly for the actor).

Pseudo-pregnancy: In all canid species, ovulations that do not result in pregnancy are obligatory followed by a period of pseudopregnancy, with the same length (2 months) and a similar hormonal profile as a true pregnancy. Particularly an increase in prolactin and oxytocin determines maternal behaviour, mammary development and milk production, and allonursing was observed in almost all canid species. Non-domestic canids are monoestrous. [2,17,25]