The unfulfilled potential of dogs in studying behavioural evolution during the Anthropocene

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ABSTRACT
Dogs are an exceptional resource for studying ecological, behavioural and evolutionary processes, but remain under-represented within these fields due to the anthropomorphisation of dog behaviour, and the view that dog domestication was human-driven. These widespread misconceptions limit our understanding of dog behaviour and inhibit the use of dogs as study systems in diverse areas of biological sciences. Here we argue that dogs should be studied using species-general fundamental principles of ecology and evolution. Specifically, two of Tinbergen's four questions remain critical, yet understudied, in understanding dog behavioural traits: 1) What is the current value of these behaviours, and 2) How did they arise and evolve? We review dog behaviour in a range of ecologies beyond just the pet niche and find: 1) dogs show a wide range of behavioural adaptations to human proximity, 2) the behaviour of dogs has changed rapidly within human niches, and 3) dog behaviour generally derives from pre-existing variation in their ancestral species, wolves. Resituating dogs within biological research will: 1) advance behavioural genetics and genomics, 2) help establish how certain species are able to adapt to anthropogenic environments where so many fail, 3) enable dogs to serve as model organisms in a range of sciences.

1.INTRODUCTION

Dogs have been of interest to scholars since Darwin (1) discussed their behavioural and morphological variation in *On the Origin of Species*. The earliest explorations of dog behaviour and psychology considered dogs through a strongly anthropomorphic lens. For example, Darwin considered the possibility that dogs possessed a religious sense in *The Descent of Man* (2) and his neighbour Sir John Lubbock published a pair of papers on "teaching animals to converse" in which he trained his pet dog to pick up cards with words written on them to convey its desires (3,4). A less anthropomorphic research program on dogs was initiated by Pavlov (5,6), but this research was less interested in dogs in their own right and viewed them more as a model subspecies in which to investigate a universal process of behavioural conditioning. A revival of interest in research on dog psychology and cognition occurred at the end of the last century with studies of the putatively unique ability of dogs to follow human pointing gestures (7,8). This focus on cognitive skills that dogs might share only with humans re-established an anthropomorphic approach to dog behaviour that has dominated the field ever since.

In this review we provide a counterpoint to the predominant anthropomorphic approach to dog research. Our goal is to resituate dogs within an objective and biological research framework, as animals whose behaviour is adapted to human-dominated niches, but is not meaningfully "human like" (cf. (9–11)). Dogs and humans have lived in symbiosis for over 15,000 years (12), but that does not imply that the fundamental principles of evolutionary, ecological and behavioural analysis are not the most appropriate ones to understand this relationship. Specifically, two of Tinbergen's (13) four questions remain essential to progress in

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understanding dogs within the human niche: 1) identifying the current adaptive value of dog behaviours, and 2) understanding how these behaviours could have arisen and evolved. Unfortunately, these questions have not been at the forefront of contemporary dog behavioural research, which has led to an under-emphasising of research on the basic ecology of dogs and a prioritisation of anthropomorphically-motivated studies.

1.1 The unique evolutionary history of the dog
During the Anthropocene, the domestic dog has arguably the largest cultural and societal impact of any animal species (14–16). Dogs were domesticated from now extinct wolf (*Canis lupus*) lineages (17,18) during the last ice age, 40,000-15,000 years ago (12). The dog is the first domesticated species of any kind and remains the only domesticated large carnivore. This combination of factors makes the dog's history of domestication unique and it should therefore be considered in a class of its own. Unlike other domesticated animals, which were adapted to human proximity primarily to supply our ancestors' need for meat (19), some wolves likely adapted to human proximity in order to scavenge on human residues and, at least initially, their development of behaviours that people found advantageous was purely serendipitous from the human perspective (15). These likely included alarm and guard functions as well as aiding hunters as the climate warmed and landscapes became more dense and difficult for humans to hunt in (20). Some authors refer to the process by which certain wolves adapted to thrive in human-modified environments as "self-domestication" (e.g., (21)). However, we see no need for a neologism to label this process. Following Darwin's (1) discussion of domestication and his distinction between artificial and natural selection, the initial process that gave rise to dogs aligns with the criteria for natural selection – albeit natural selection in service of adaptation to human-modified niches.

1.2 The majority of present-day dogs do not belong to the pet niche
Although dogs are most familiar to observers in the first world as pets, typically living inside human homes and intentionally provisioned by human hosts, this pet niche is only one of three in which dogs live, and far from the most common one on a global scale (Fig. 1). Estimates vary widely, but of the likely 800,000 to 1,000,000 dogs alive at the present time (22), only around 17-24% live inside homes as pets (23–25). The approximately 80% of dogs not living as pets are free-ranging, free-breeding dogs that can be grouped into two broad classes (Fig. 1). The larger of these populations are the scavengers. These dogs do not live in human homes, but nevertheless depend on food provided inadvertently by humans. This scavenger group ranges from dogs who may still be perceived as the property of certain people and be provisioned and named by them, through to dogs who live in proximity to humans and obtain most of their nutrition by scavenging for food on human waste while avoiding direct contact with people (26,27). Finally a smaller population of dogs subsists as true hunters, not reliant on human-originating food sources (28–30). Transitions between these populations are possible, as pets may be rejected by their human hosts and become scavengers, just as scavengers may be adopted into human homes as pets (28). The hunter population is probably more isolated from other dog groups because, if not exposed to people early in life, they cannot easily adapt to the closer human proximity needed for successful scavenging. However there is evidence that scavengers are recruited into hunter populations (31,32).
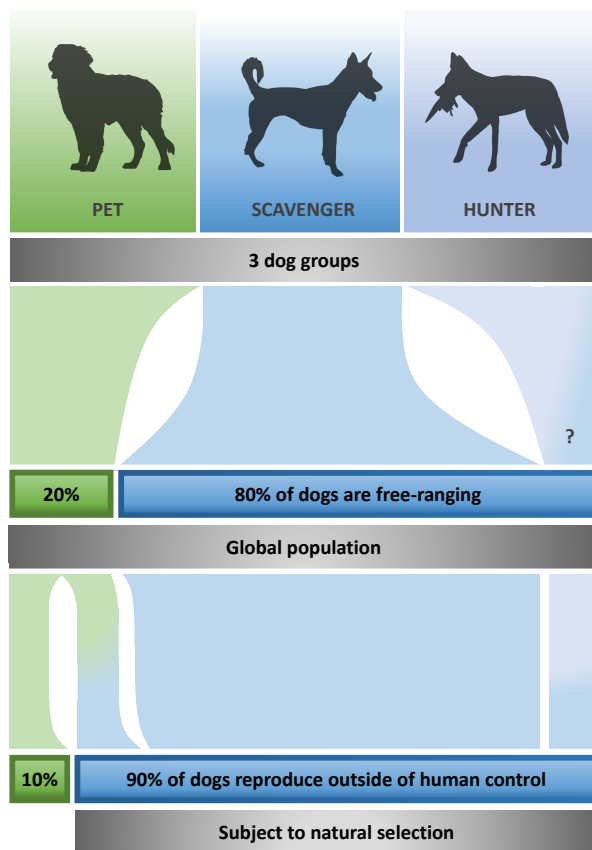
Figure 1. Of the three dog groups 1) Pet, 2) Scavenger and 3) Hunter contributing to the global dog population, 80% live as free-ranging dogs. Both the Scavenger and the Hunter groups contribute in their full extent to the free-ranging part of the global dog population. The extent of the Hunter group, and thus how much it contributes to the proportion of the free-ranging dog population, is unknown (indicated by a question mark). Only a minority of dogs live in human homes and these dogs all belong to the Pet niche. The Pet niche is estimated to amount to 20% of the global dog population. Of the total global dog population, it is estimated that the reproduction of 90% of dogs is not under human control. This includes half of the current Pet dog population (Unedited images from PhyloPic, credits Margot Michaud and Gabriela Palomo-Munoz: licensecreativecommons.org/licenses/by-nc/3.0/).

1.3 Dogs are subject to natural selection

The widespread assumption that humans significantly influence dog breeding, creates a misleading impression of the role of humans in dog reproduction at a population level (33,34). However, a study in the United States, where most dogs live in households as pets, estimated that only 50% of matings were under human control (35). If this value holds for the rest of the developed world, it would imply that world-wide only around 10% (50% of the 20% of dogs that live as pets) of dog matings are the outcome of artificial selection: The remaining 90% of dogs worldwide are subject solely to natural selection (Fig. 1). Thus, it is likely the case that, contrary to the widely expressed opinion that dogs today are primarily the outcome of artificial, human-directed, reproduction (33,34), natural selection remains a major force in dog evolution in the modern world.

2. SOCIAL BEHAVIOUR IS KEY TO DOGS' ADAPTATION TO THE HUMAN NICHE

For dogs in the pet and scavenger niches (i.e., the majority of dogs), tolerance of human proximity must be the main driver for successful adaptation as it makes mutual tolerance and close partnerships with people possible. This capacity for inter-species sociality thus affects virtually all aspects of these dogs' lives.

2.1 Pathways to dog's social adaptations to living in human proximity

Behavioural adaptations may arise through three, not necessarily mutually exclusive, pathways. First, it is well-established that evolutionary change relies heavily on standing genetic variation (e.g., (36,37)). Advantageous behaviours can become widespread in domesticated populations due to selection on pre-existing variation in ancestral, wild, populations. The potential for domesticated phenotypes to derive from pre-existing variation

in wild populations is exemplified in the Farm Fox project in which red foxes (*Vulpes vulpes*) were artificially selected over generations for tameness towards humans (38,39). Specifically, prosocial behavioural characteristics which became common in the selected, domesticated, foxes – as expressed by reduced fearful and aggressive responses towards humans – can be observed at a low frequency in the ancestral, wildtype, population (40).

Second, novel mutations may occasionally give rise to changed behaviour. This may be evident, for example, in the evolution of hyper-sociability in the dog through changes in genes which in humans give rise to Williams-Beuren syndrome (41). Williams-Beuren syndrome is a rare genetic disorder involving deletion of genetic material from a region on chromosome 7 (42). It has a wide variety of phenotypic effects including excessive gregariousness or hypersociability (43). vonHoldt et al., (41) demonstrated that the enhanced sociability of dogs towards familiar and unfamiliar humans relative to hand-reared wolves was related to mutations in three genes implicated, in humans, in Williams-Beuren syndrome. However, while this may be a possible route to altered behavioural expression in dogs, instances of this type are expected to be extremely rare since complex phenotypes, such as behavioural traits, likely are caused by many genes of small effect (44,45). Repeated non-deleterious mutations in functional regions of the genome across multiple coding regions are thus very unlikely.

Finally, and surely of particular importance in the case of complex, cognitive behaviours, novel patterns of action may arise through the co-option of general behavioural processes. Basic behavioural processes of great relevance when considering dogs in human contexts include social imprinting, and Pavlovian and operant conditioning. These processes are present in a wide range of animal species (see e.g., (46,47), for reviews), but the specific patterns of behaviour they give rise to depend on the environment experienced by individuals. Consequently, quite distinct behavioural patterns may be observed in individuals of the same or different species that are nonetheless the outcome of the same basic process. This fact is often obscured by an enthusiasm among researchers to label patterns of behaviour as if they are always evidence of distinct phenotypes. Blumberg and Wasserman (48) identified this as a form of the nominal fallacy — the belief that naming something amounts to an explanation. Treating each name-able behaviour pattern as a phenotype makes it difficult to identify the level at which a behaviour needs to be explained and often confuses the boundaries of phylogenetic vs. ontogenetic effects (49).

2.2 Understanding the origins and adaptive value of social behaviours in dogs

Clarifying whether social behaviours expressed in dogs are based on selection upon standing variation from ancestral wolf lineages, novel mutations, or conditioning of novel behavioural patterns is crucial for understanding the evolutionary history of these behaviours as well as their current adaptive value. Because the underlying genetic causation for behavioural phenotypes is highly complex (44,45), comparing behaviour in wolves and dogs is often the only way to gain information about evolutionary processes during domestication. However, differentiating between the three paths to behavioural adaptation using wolf-dog comparisons is made difficult by the small sample sizes, particularly of wolves, used in this research. As standing ancestral variation for behavioural traits expressed in present-day wolves is likely to be rare (50), the small numbers of wolves typically tested can lead to this species appearing to lack behavioural characteristics easily observed in dogs. Thus it is crucial to test an adequate number of wolves to draw defensible conclusions about the evolutionary origins of the behaviours seen in present-day dogs. To illustrate this point we draw on a well-documented example from outside the behavioural literature: Initially it was thought that dogs had an increased copy number of the amylase locus (AMY2B) compared to wolves and it was

proposed that this was an early novel adaptation to a starch-rich diet in post-domestication dog lineages (51). However, subsequent sampling of additional wolves revealed standing variation in amylase copy numbers, thus flipping the evolutionary narrative of AMY2B from being a case of evolution by novel mutation to one of selection upon standing ancestral variation (17). Additionally, studies comparing behaviour in wolves and dogs often only report mean values of traits per species (52–55). However, this practice will mask rare behaviours and thus overlook individual variation in wolves and consequently miss standing ancestral variation. Continuously disregarding these factors prevents us from adequately disentangling selection dynamics during initial dog domestication, hindering our understanding of the evolutionary underpinnings of dog behaviour.

3. DOG BEHAVIOURAL AND SOCIAL ADAPTATIONS TO HUMAN CONTEXTS

In this section we review domains of social behaviour relevant to dog-human coexistence with a particular focus on Tinbergen's questions of evolutionary origin and current adaptive values, keeping in mind the three pathways by which novel behaviour may arise.

3.1 Point & Gaze Following

Dogs' abilities in following human pointing gestures were among first social behaviour patterns proposed as unique cognitive adaptations to living in human proximity (7,8). The initial apparent absence of this behaviour in wolves (52,56) encouraged the view that it represented a special adaptation to living near humans. Subsequently, appropriately hand-reared wolves have been found competent in following human pointing gestures and, to date, 28 different species including both domestic and wild lineages across at least eight taxonomic groups have been shown to successfully follow pointing gestures given by humans (57). Rather than a *de novo* mutation, point following is an excellent example of a universal behavioural process, most likely Pavlovian conditioning, that develops in the specific ontogenetic environment of particular individuals rather than a direct outcome of phylogenetic change (57,58).

Similar to the ability to follow human pointing gestures, is the ability to interpret human gaze direction as shown through gaze-alternation and -following. This shifting of head orientation and eye movement, or the monitoring of these orientation shifts and movements in others, is used to communicate intentions as well as to receive information about the environment (59). When raised and tested under similar conditions, dogs and wolves demonstrate similar abilities to engage and direct human helpers to locate an out of reach food source by gaze alteration (60). Furthermore, wolves have fully developed skills in following human gazing into distant space at the age of 14 weeks (59). Studies suggest that wolves might also develop the ability to follow human gazing around barriers before 4-5 months of age, which has also been demonstrated in ravens and rooks (59,61,62). In sum, similarly to point following, the fact that an ability to follow gazing has been demonstrated across taxa, suggests that this capacity develops through ontogenic rather than phylogenetic processes.

3.2 Attachment behaviours

Attachment is defined as an enduring bond between two individuals based on emotional dependency that endures over time (63,64). In altricial species there is a strong adaptive value in bonding between young and attachment figures, usually one or both parents, because it ensures not only survival through fulfilment of basic needs, such as food and protection, but also the acquisition of independence as the young animal is provided with a secure base from which it can explore new environments (64,65).

Various studies have confirmed through the standardised Strange Situation Test (SST) that the human-dog bond can be compared to the parent-offspring attachment bond in humans (66–71). In these tests, dogs' affiliative, distress and exploratory behaviours are compared in social situations with a caregiver and a stranger. Pet dogs living in human households typically express more affiliation and engage in more exploratory behaviours in the presence of their caregiver and express distress upon separation from him or her. Human-directed attachment behaviours have also been found in working dogs (72,73) and owned village dogs allowed to roam free (74).

Initial studies on attachment behaviour in wolves (53,53) concluded that they were unable to discriminate between caregivers and strangers and lacked the capacity to show attachment toward familiar people in the same manner as dogs. However, more recent studies have demonstrated human-directed attachment behaviours in hand-reared wolves across various age groups. Hall et al. (75) showed that wolf puppies up to the age of eight weeks discriminated between a strange and a familiar person in the SST by engaging in significantly more proximity- and contact-seeking toward a familiar caregiver. Using a simple greeting test, Ujfalussy et al. (76) showed that wolves aged six, 12, and 24 weeks expressed affiliative behaviours toward a familiar person and readily discriminated between familiar and unfamiliar people. Similarly, Lenkei et al. (77) demonstrated in a separation test how adult wolves expressed increased contact seeking behaviour and secure base effects in the presence of a familiar person. Finally, in a recent study, Hansen Wheat et al. (78) showed that 23-week-old wolves and dogs discriminated equally between a stranger and a familiar person in the SST, and expressed similar levels of attachment behaviours toward a familiar person. This study also demonstrated how wolves used the familiar person as a social buffer in stressful situations, lending further support to the observation that wolves express attachment toward familiar people.

The collective evidence from recent studies quantifying attachment behaviours in wolves indicates that they indeed have the capacity to express attachment toward humans. Consequently, this capacity in dogs could be derived from standing variation in ancestral wolf populations, or could even be evidence of an ability based on a broadly available behavioural process that might be observed in other species. For example, Vitale et al. (79) reported attachment behaviour towards humans in pet cats.

3.3 Cooperation
Dogs' readiness to cooperate with humans in a range of domains, from hunting to guide dogs for the blind is often remarked upon (55,80), but before reviewing research on dogs' cooperation with humans we first consider cooperation among dogs. Cooperation can be defined as, "behaviour in which members of a species combine in an activity" ((81) p. 41).

3.3.1 Conspecific cooperation
There is surprisingly little evidence of a willingness to cooperate with conspecifics in dogs, outside the domain of play (see section 3.3.3 below) particularly when compared to wolves. In a direct test of dogs' and wolves' readiness to cooperate using subjects drawn from similarly human-reared groups, Range et al. (82) offered a potentially monopolizable food item to pairs of dogs and pairs of wolves. They found that in each pair the dominant wolf, but not the dominant dog, tolerated feeding by the subordinate individual. Similarly, Dale et al. (83) using study subjects from the same populations, reported that pairs of wolves, but not dogs, shared a carcass. In each study, subordinate dogs, unlike subordinate wolves, were almost entirely prevented from feeding by the dominant individual in each pair.

Ostojić and Clayton (84) tested pairs of pet dogs living together in a human home on a string-pulling task which required two individuals to pull simultaneously, each on one end of a string, for either of them to receive a food reward. Animals in this study showed no spontaneous tendency to cooperate in solving the task but were successful after extensive training. Marshall-Pescini et al. (85) replicated this study using the hand-reared but group-housed dogs and wolves previously tested in Dale et al. (83) and Range et al. (82). Marshall-Pescini et al. (85) found that, although levels of engagement with the task were similar in the two species, only the wolves successfully cooperated and obtained the available food. Marshall-Pescini et al. (85) suggested that the success of Ostojić & Clayton's dogs on the same task was due to human intervention ensuring quiescent cooperative behaviour in dogs living together in a human household, combined with the training to encourage cooperation.

Bräuer et al. (86,87) studied cooperation in pairs of pet dogs and wolves using a task in which the animals had to pass through one of two doors in a transparent fence barrier in order to access a food treat. The door openings were arranged so that the only way for dogs and wolves to get at the food was for one of them to approach an opening while the other passed through the barrier, and then the first animal had to wait for the door it stood in front of to open. Both dogs (86,87) and wolves (87) were reportedly successful to similar levels of performance on this task. However, there was no evidence that individuals from either species were attending to the behaviour of their partners in these studies. In other words, the canids were solving this ostensibly cooperative task in a non-cooperative manner.

Few studies have been carried out on cooperation in free-ranging dogs, but it has been observed in Kolkata, India that free-ranging dogs forage both individually and in groups (88). When foraging individually, they seek to maximise both the quality and quantity of food sources (89), but at the cost of increased vigilance behaviour (90). In groups, free-ranging dogs show less selectivity of food resources and reduced vigilance, with more efficient exploitation of food patches (90). These results align with general group foraging theory (91,92), and suggest that free-ranging dogs express phenotypic plasticity in cooperation strategies when it comes to foraging.

Cooperation with conspecifics is an interesting case of a behaviour that is well-developed in wolves, but appears to have been attenuated during domestication in a manner consistent with the divergent foraging ecology of wolves and dogs. Wolves subsist by hunting live prey that are often larger than themselves and which can only be captured by the coordinated activity of a group (93,94). Once brought down, the amount of meat offered by common wolf prey species is typically more than one individual could consume alone (93). Since members of a wolf pack are closely related, dominant individuals have no adaptive motivation to attempt to monopolise the food source: Consequently cooperation is widespread in wolves. Dogs on the other hand, primarily scavenge on human food residues (26,29). These do not typically require any coordination with group members to procure and are also often distributed in quantities that are small enough to be monopolised by individuals (89). The looser social organisation of free-ranging dogs, which may associate in transitional to stable packs but do not live in family groups (23,95–97), thus allows for larger plasticity in foraging strategies.

Conspecific cooperation is thus an example of ancestral behaviour lost during dog domestication likely due to the changed foraging ecology of the domestic animal relative to its wild ancestor.

3.3.2 Human-directed cooperation

Although conspecific cooperation is less pronounced in dogs than in wolves, it is widely remarked that dogs very readily cooperate with humans (e.g., (55)). However, it is difficult to demonstrate relative willingness to cooperate with humans by different species because very few attempts have been made to bring individuals from non-domestic species and subspecies into cooperative arrangements with people. Two relevant studies were carried out on similarly-hand-reared wolves and dogs using the string-pulling task described above (section 3.3.1). Range et al. (98) directly compared the willingness of wolves and dogs to cooperate with familiar people and found that on average wolves performed slightly but significantly above chance, whereas the performance of dogs was not significantly above chance. However, in a complete analysis, the effect of species was not significant. Interestingly, the wolves and dogs adopted different strategies on the task, with wolves more inclined to take the lead in selecting a string to pull on, whereas dogs were more likely to follow the human partner's lead. Given the large difference in levels of cooperation between wolves and dogs when they are tested on this same task with a conspecific partner, the relatively modest differences when they are tested with a human partner are very thought-provoking and worthy of further study with other cooperative paradigms. In a subsequent study using animals from the same populations and the same string-pulling cooperative task, Range et al. (99) tested the animals' comprehension that a partner was needed to successfully complete the task. Again, they found no overall difference between dogs and wolves. These findings are remarkable in view of the widespread belief that dogs have an exceptional affiliation with humans and more studies are needed to clarify the conditions under which dogs and wolves may cooperate with people.

The studies on dogs' ability to follow human indicative gestures noted above (section 3.1), have been offered as evidence of human-directed cooperation (7,8), but the substantial evidence that suitably hand-reared wolves can match dogs' success on these tasks indicate that this form of cooperation with humans relies on behaviours that predate domestication.

3.3.3 Play behaviour.

Dogs show considerable evidence of cooperation in social play. In most species, play is predominantly expressed in juveniles, but in dogs and other domesticates, playful behaviour is also observed in adult individuals. This has been hypothesised to be an indirect result of paedomorphism, i.e., the retention of juvenile characteristics into adult life (45,100–102), However, since play still occurs albeit at attenuated levels in adult non-domesticated animals (103–105) a continued adaptive value of this social behaviour beyond juvenile ontogenetic stages must exist, likely related to competition or cooperation (106).

3.3.4 Conspecific play

Dog puppies initiate playful fight interactions with their littermates as early as 2-weeks-old at the onset of the socialisation period (107). To ensure continuation of a play bout and prevent injury, dogs commonly express cooperative play strategies such as self-handicapping or role-reversals, in which they let themselves be more vulnerable to advances from the play partner. An otherwise dominant individual may also adopt a submissive role (106). Self-handicapping and role-reversal have been demonstrated in both juvenile (108) and adult dogs (106). These findings indicate that play in dogs is truly cooperative and not hindered by skewed dominance relationships or uneven displays of self-handicapping and role-reversal.

Only a handful of studies have directly compared the ontogeny of conspecific play behaviour between wolves and dogs (109–114). These studies vary in their conclusions, likely due to small sample sizes, and possibly the use of different dog breeds. Earlier studies reported more play in dog puppies than in wolves (109) and more pronounced agonistic play in dogs compared

to wolves (113). However, Feddersen-Petersen (111) followed three litters of wolves and three litters of poodles for a year and found that the wolves began to play earlier than the poodles and remained more playful throughout the first year of life. Notably, the poodles showed a sharp decline in play behaviour around six months of age when their interactions became more agonistic. This shift was not seen in wolves. A more recent study compared play solicitation in juvenile wolves and dogs and found that the frequency of play bowing was not significantly different between wolves and dogs before eight months of age. However, where bows in playing dog dyads tended to entice more active play, this pattern was not found in wolf dyads (114).

Like dogs, wolves commonly retain social play into adulthood (103,115–117). Play fighting is more frequent between wolf pack members of unclear relative dominance rank (103,116), which supports the hypothesis that social play, by providing access to information about relative vigour, prevents potentially harmful aggressive encounters (118,119). While it remains unresolved if this adaptive strategy is also adopted by dogs (120), overall the literature does not suggest that the underlying patterns of conspecific play in dogs differ substantially from those observed in wolves.

3.3.5 Human-directed play

Dogs' willingness to cooperate with humans is also seen in their frequent engagement in human-directed social play (121–123). Play solicitation in dog-human dyads is bidirectional, with humans engaging dogs in social play by imitating conspecific initiation signals such as the play bow, but also by using a lunge-signal unique to dog-human interaction (122). Likewise, dogs have been observed to actively re-engage a human play partner after an interrupted play session by increasing physical contact and offering a play toy to this partner in a choice test in preference to a passive test person (123). Dogs modify their play-behavioural repertoire when playing with humans when compared to playing with conspecifics (121). Furthermore, in social object play, dogs in dog-dog dyads showed more competitive object possession whereas interactive object presentation by the dog predominated in dog-human dyads (121).

Hansen Wheat et al. (124) compared human-directed play in dog-wolf hybrids, dogs from the breeds in these hybrids (Siberian Husky, Alaskan Malamute and German Shepherd), as well as in a dog breed with a more dilute wolf component, the Czechoslovakian wolfdog. This study demonstrated least playfulness in the wolf-dog hybrids, highest playfulness in the dogs, and intermediate levels in the Czechoslovakian wolfdogs. Although this result suggests that human-directed play may be less common in dogs with higher wolf content, this does not mean that wolves do not play with humans. Human-directed play has been observed in human-reared wolves. Hansen Wheat and Temrin (50) invited 13, 8-week-old hand-raised wolf puppies without prior training to fetch a tennis ball for a stranger. Three of the puppies spontaneously fetched the ball and engaged in human-directed play with this unfamiliar person. These results indicate that fetching, one of the most frequently reported play interactions owners engage in with their dogs (125,126), though likely rare, is a behavioural phenotype that exists in wolves. Human-directed playfulness in dogs could therefore originate in standing variation in ancestral wolf populations (50).

Play stands out from other types of cooperation in dogs for the high frequency with which dogs cooperate both with conspecifics and with humans. However, the clear evidence for play in wolves — even in some cases with humans — indicates that this behaviour in dogs likely originates in pre-existing variation in wolves. This also suggests that playfulness as a trait was

under positive selection during early dog domestication (124,127). If engaging in playful interactions with humans presented an adaptive advantage to early dogs, then the cooperation inherent in play may have offered a pathway towards other forms of human-directed cooperation that are central to the dog-human relationship as it is experienced today.

4. THE DOG AS A MODEL SPECIES

Dogs are a widely-used model species within human medical research, including studies on cancer (128), gene therapy (129) and hereditary diseases (130,131). However, while dogs could provide an equally powerful model species for rigorous evolutionary and ecological research, their potential remains mostly overlooked. Furthermore, one particularly exciting and timely avenue for dog models is in the field of urban evolution, where different populations of dogs can be used to uncover how urbanisation selects upon behaviour in large vertebrates. Another important field where advances to date have proven elusive is behavioural genetics. The behavioural diversity among dog breeds, combined with a recent explosion in genomic tools, has led to some progress, however, dog models could also provide much needed insights into the interplay between populations and behavioural genetics.

4.1 Urban Ecology and Evolution

As the majority of present-day wild species are living in environments influenced by anthropogenic change (132), research addressing behavioural responses to urbanisation is urgent. While the field of urban ecology is still in its infancy (133,134), it is clear that urbanisation is a powerful influence on behavioural phenotypes. For example, the timing and duration of breeding seasons and foraging behaviour can be modified by urban environments (135), and behavioural syndromes can change, or even break down, between rural and urban environments (136,137). Because the present-day dog population is so abundantly represented world-wide and so well-adapted across a range of niches with varying degrees of anthropogenic interference, dogs, given their evolutionary history, might be the best current model for in-depth investigations of how urbanisation selects upon behaviour. Their diverse strategies in profiting from human proximity contrast interestingly with other canid species that have found alternative paths to adaptation to anthropogenically altered environments such as coyotes (*Canis latrans*) and foxes (see (138) for a review).

4.2 Behavioural Genetics

Uncovering the genetic basis for complex traits, such as behavioural phenotypes, is challenging. However, dog breeds provide an excellent opportunity to study behavioural genetics. There are approximately 400 registered dog breeds in the world today (139), of which the majority originated as recently as in the Victorian era and are less than 200 years old (139–141). These modern breeds were, and are still today, bred for highly specialised behavioural and morphological traits following rigorous breed standards, yet the breeds are significantly introgressed. This provides an ideal model set-up for behavioural genetics studies.

Two recent large-scale behavioural genomic studies on breed (44,142) and mixed breed dogs (142) provide new insights into the origin of the behaviour of present-day dogs breeds. Dutrow et al. (44) used a combination of whole genome sequencing and single-nucleotide polymorphism array data from more than 4,000 domestic dogs, village dogs, and wild canids as well as behavioural survey data on over 46,000 dogs and identified multiple genomic regions possibly related to domestication behaviours. This included haplotype blocks with ancient signatures, suggesting that these behaviours could have existed in early dogs. Morill et al. (142) combined more than 18,000 behavioural assessments from dog owner surveys with genome-wide associations analyses of 2155 dogs and found that a single SNP on Chromosome 2 was

associated with human-directed sociability. Although modern breed dogs are unsuitable for answering questions about early dog domestication, as they are poor representatives of the original dogs from a genetic and behavioural perspective (44,140,143), nonetheless the identification of such genomic regions possibly related to behaviours relevant to domestication is encouraging. Both studies emphasised that canine behavioural diversification predates modern breed formation and is assumed to have originated through selection over thousands of years. Importantly, this scenario aligns with the assumption that the origin of key behaviours, such as herding, seen in present-day dogs is based upon standing genetic variation among ancestral wolf populations (44).

5. CONCLUDING REMARKS

Although the dog is thoroughly integrated into human society, it still has a well-defined species ecology. Importantly, we estimate that although 90% of the global dog population is subject to natural selection through uncontrolled breeding, the majority of research on dogs has been, and still is, carried out on the minority of dogs belonging to the pet niche. Further, the research reviewed here demonstrates that while present-day dog behaviour is highly adapted to the human niche, since these behaviours can also be observed, albeit at a lower frequency, in wolves, the most parsimonious explanation is that many dog behaviours have evolved from standing variation in ancestral wolf populations.

Dogs fully fulfil the criteria warranting their study using established paradigms for behavioural ecology and evolution. We highly encourage new research efforts on dogs within this framework, with particular focus on the relatively neglected free-ranging majority of the global dog population, in preference to the over-anthropomorphized research on pet animals that currently dominates the field.

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