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. However, several widespread misconceptions limit our understanding of dog behaviour and inhibit the use of dogs as model study systems in diverse areas of biological science. These include extensive anthropomorphisation of dog behaviour, a profound bias towards almost exclusively studying pet dogs, a widespread belief that dog domestication was human-driven and that the majority of dogs are not subjects of natural selection. Here we argue that dogs should be studied using species-general fundamental principles of ecology and evolution, and that the focus in dog research should shift towards free-ranging dogs, which comprise ~80% of the global dog population. By focusing this review primarily on the available literature on free-ranging dog behavioural ecology we find that: 1) 90% of all dogs today breed

without human interference, 2) free-ranging dog populations express substantial variation in their behavioural ecology across their global range, and 3) many aspects of dog behavioural ecology have likely evolved from standing variation in ancestral wolf populations. With the dog objectively placed within a biological framework, it becomes clear that the large behavioural variation expressed across free-ranging dog populations is key to understanding dogs' great success in the rapidly developing anthropogenic niche. Since free-ranging dogs have a global distribution across various environmental gradients, including urbanization, climate and social structures, they provide an ideal opportunity to collect comparable, large-scale data across populations. Combined with the in-depth knowledge of dog evolutionary history and the advanced genetic tools specifically developed using the species, dogs can be an outstanding model for the study of urban ecology and evolution.

1 INTRODUCTION

Dogs have interested scientists since Darwin (1859) discussed their behavioural and morphological variation in *On the Origin of Species*, but the earliest explorations viewed dog behaviour through a strongly anthropomorphic lens. Darwin himself (1871) considered the possibility that dogs possessed a religious sense, and his neighbour, Sir John Lubbock, published a pair of papers explaining how he trained his dog to pick up cards with words written on them to convey its desires (Lubbock, 1884a, 1884b). Pavlov initiated a less anthropomorphic research program using dogs in the 1890s (Pavlov, 1927), but this research focused on the universal process of behavioural conditioning, and was not concerned with exploring dog behaviour *per se*. After a brief focus on dog behavioural ontogeny, culminating in Scott and Fuller's *Genetics and Social Behavior of the Dog* (Scott & Fuller, 1965), interest in dog behavioural research declined until an abrupt revival at the end of the last century (Aria

et al., 2021). While these new studies have a range of purposes, including understanding dog domestication (e.g., Marshall-Pescini et al., 2017; Hansen Wheat et al., 2019) and behavioural genomics (e.g., Chen et al., 2021; Dutrow et al., 2022; Morrill et al., 2022), studies focusing on cognitive skills that dogs might share only with humans have re-established an anthropomorphic approach to dog behaviour that now dominates the field (e.g., Buttner, 2016; Duranton & Gaunet, 2018; Hare et al., 2002; Hare & Tomasello, 2005; Topál et al., 2009).

Our goal with this review is to highlight the potential of the dog as a species for studying behavioural ecology and evolution in the Anthropocene. As the majority of present-day wild species live in environments influenced by anthropogenic change (Sih et al., 2011), research addressing behavioural responses to urbanisation is urgent. Urbanisation has a substantial effect on behavioural phenotypes. For example, it can influence the timing and duration of breeding seasons and foraging behaviour (Lowry et al., 2013) and the expression of behavioural syndromes can change, or even break down, between rural and urban environments (Bókony et al., 2012; Scales et al., 2011). Because the present-day dog population is represented on every continent with permanent human habitation across a wide range of ecological niches with varying degrees of anthropogenic interference, dogs may be the best current model for in-depth investigations of how urbanisation selects upon behaviour. Although many species express high levels of adaptation to anthropogenically-altered environments, no other species offers the unique set of qualities ideal for global, integrated, large-scale studies like the dog.

We will argue, however, that dogs' potential contribution to understanding adaptation to the Anthropocene has been stymied by multiple factors including excessive anthropomorphism, an over-reliance on pet dogs, and a failure to recognize that dogs are subject to natural selection,

among others. These systematic biases inhibit the full potential of insights to be gained from studying dogs.

In order to place dogs within an objective biological research framework, as animals whose behaviour is likely adapted to human-dominated niches, but is not meaningfully "human like" (cf. Buttner, 2016; Duranton & Gaunet, 2018; Hare et al., 2002; Hare & Tomasello, 2005; Topál et al., 2009), we will review their behavioural ecology with focus on 1) identifying the behavioural variation across dogs populations, and 2) understanding how this variation could have arisen and evolved. In doing so, this review will emphasize the value that studies of under-represented dog populations can have for other species. While dogs are a widely-used model species within human medical research, (e.g., cancer (Gardner et al., 2016), gene therapy (Switonski, 2014) and hereditary diseases (Correard et al., 2019; Hytönen et al., 2019)), their potential as equally powerful models in evolutionary and ecological research remains mostly overlooked.

Below we outline this rich potential of dogs by emphasizing the vast variation in behavioural ecology of the species seen across different anthropogenic environments, while drawing as much as possible on examples from the free-ranging dog population. This will ultimately illustrate the wide range of conditions to which the dog has likely adapted, which together with its widespread global distribution and unique and well-studied evolutionary history makes the dog an ideal model species for studies in urban ecology and evolution (*sensu* Verrelli et al., 2022).

2 RECALIBRATING OUR UNDERSTANDING OF THE DOG AS A SPECIES

Dogs are one of the most popular pets in the Western world, where they are often referred to as family members, and the cliché "dog is man's best friend" (ascribed to Frederick the Great and Voltaire, (Laveaux & King of Prussia, 1789; Voltaire, 1824)) captures much of how this animal is perceived in popular culture. Unfortunately, these images of dogs as human creations and human-like companions have also dominated the recent scientific literature on dogs. We outline here important ways that our perception of dogs needs to be recalibrated.

In this section we place the dog within an objective biological research framework by addressing the following misconceptions: 1) identifying that dogs have a unique history of domestication that does not primarily depend on artificial selection; 2) clarifying that only a minority of dogs can be classified as pets; 3) demonstrating that the vast majority of dogs, even today, are subject to natural selection; and 4) concluding that the sum of these misunderstandings is a distorted view of dog behaviour.

2.1 Wolf Exaptation and Adaptation to Early Human-Modified Niches

The evolutionary history of the dog is unique. Domesticated from now extinct wolf (*Canis lupus*) lineages (Bergström et al., 2020; Freedman et al., 2014) during the last ice age, 40,000-15,000 years ago (Perri et al., 2021), the dog is the first domesticated species of any kind and remains the only domesticated large carnivore. Unlike the domestication of the majority of animals, such as sheep and reindeer for resource management (Russell, 2011), or horses and donkeys for transportation (Larson & Fuller, 2014), domestication of the dog was not instigated by deliberate human action (Larson & Fuller, 2014; Zeder, 2012). Though the location and timing of first dog domestication remains a matter of debate (Savolainen et al., 2002; vonHoldt et al., 2010), there is broad consensus (Coppinger & Coppinger, 2001; Larson & Fuller, 2014;

121 Zeder, 2012) that the process was initiated when some ancestral wolves with reduced fear
122 associated themselves as commensals within the new niche created by humans (Boitani &
123 Ciucci, 1995; Larson & Fuller, 2014). These less fearful wolves exapted (Gould & Vrba, 1982;
124 Winchell et al., 2023) to human proximity were able to exploit a new food resource by
125 scavenging on human refuse, and thereby represent the first known example of exaptation to
126 an anthropogenic niche. As these wolves adapted further to the human niche, some of their
127 behaviours were initially purely serendipitously advantageous to their human hosts. These
128 likely included alarm and guard functions as well as aiding hunters as the climate warmed and
129 landscapes became more dense and difficult for human hunters (Perri, 2016).

130

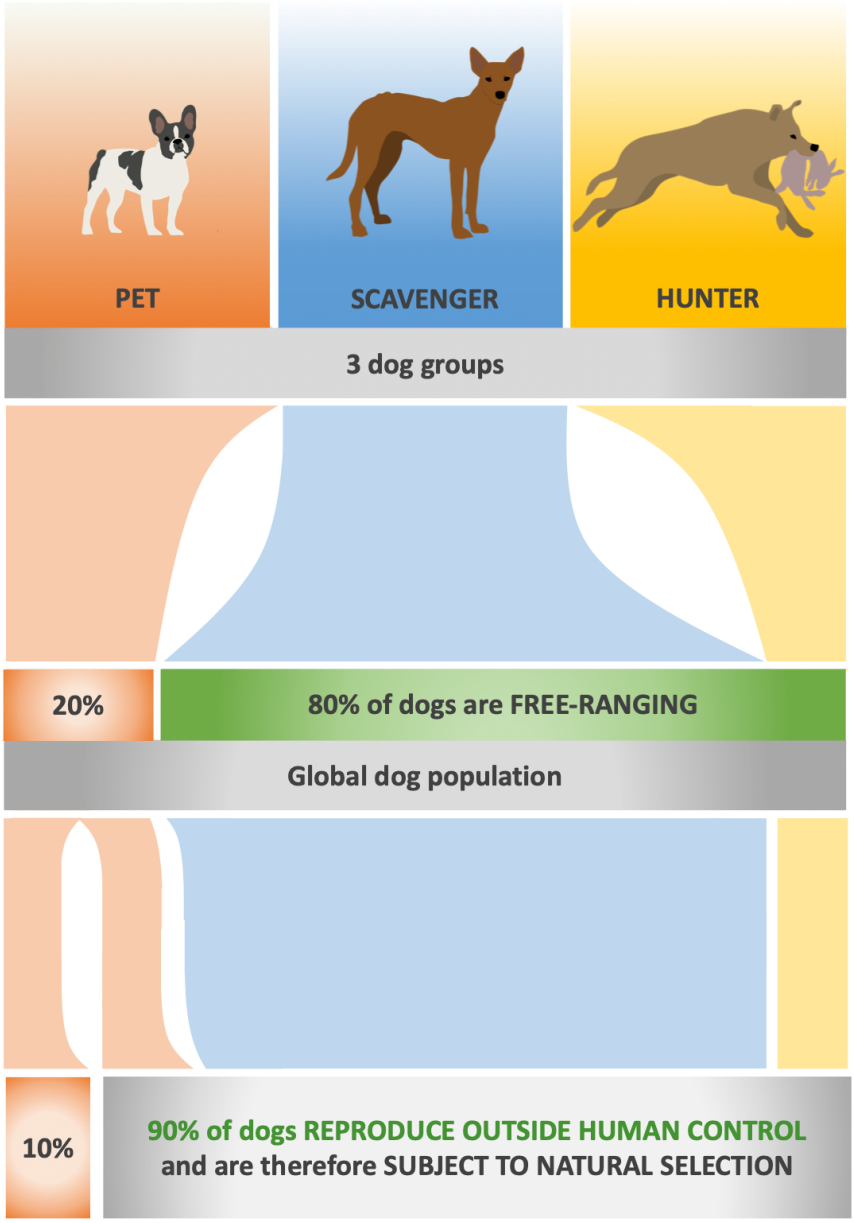
131 Some authors refer to the process by which certain wolves adapted to human-modified
132 environments as "self-domestication" (e.g., Hare et al., 2012). However, we see no need for a
133 neologism to label this process. The initial process that gave rise to dogs aligns with the criteria
134 for natural selection – individuals exapted to a new niche then further adapted to this niche.
135 Only later in the process was artificial selection applied by humans recognizing useful
136 characteristics of these animals (Ritvo, 2010).

137

138 ### *2.2 The Majority of Dogs do not Belong to the Pet Niche*

139 In the Western world, dogs are mostly viewed as pets. However, on a global scale this pet role
140 represents the minority of three niches in which dogs currently live (Fig. 1). Estimates vary,
141 but of the global dog population of 800,000 to 1,000,000 individuals (Rowan, 2020), only
142 around 17-24% can be categorized as pets (Hughes & Macdonald, 2013; Lord et al., 2013).
143 The approximately 80% of dogs not living as pets are free-ranging, free-breeding dogs that can
144 be grouped into two broad classes (Fig. 1). The larger of these populations are the scavengers.

While these dogs do not live in human homes, they nevertheless depend on food from humans. The scavenger group ranges from dogs who may still be perceived as the property of people and be provisioned by them, through to dogs who live in proximity to humans and obtain most of their nutrition by scavenging on human refuse while avoiding direct contact with people (Boitani & Ciucci, 1995; Coppinger & Feinstein, 2015; Sarkar et al., 2019). Finally a smaller population of dogs subsists as true hunters, not reliant on human-originating food sources (Coppinger & Coppinger, 2001; Duarte et al., 2016; Macdonald & Carr, 2016). Transitions between these populations are possible, as pets may be abandoned and become scavengers, just as scavengers may be adopted into human homes as pets (Coppinger & Coppinger, 2001). 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 (Scott & Fuller, 1965). However there is evidence that scavengers are recruited into hunter populations (Poyarkov et al., 2011a; Poyarkov, et al., 2011b).



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160 ***Figure 1. The current dog population.*** *Of the three dog groups 1) Pet, 2) Scavenger and 3) Hunter contributing*
161 *to the global dog population, 80% — the Scavengers and Hunters – live as free-ranging dogs. The extent of the*
162 *Hunter group is unknown. Only around 20% of dogs— all Pets— live in human homes. Of the total global dog*
163 *population, we estimate that the reproduction of 90% of dogs is not under human control and is thus subject to*
164 *natural selection. This includes half of the pet dog population. (Figure: Rasmus Erlandsson, Christina Hansen*
165 *Wheat).*

166

2.3 The Majority of 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 the population level (Hare & Woods, 2013; Miklósi, 2015). A study in the United States, where most dogs are kept as pets, estimated that only 50% of matings were under human control (New et al., 2004). If this value holds for the rest of the developed world, it would imply that world-wide only around 10% (i.e., 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 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-controlled reproduction (Hare & Woods, 2013; Miklósi, 2015), natural selection remains a major force in dog evolution in the modern world.

2.4 Overrepresentation of Pet Dogs in Research

Because pet dogs live in a very particular niche and form only a minority of the dog population, their overrepresentation in dog behavioural research (Bauer & Smuts, 2007; Duranton & Gaunet, 2018; Dutrow et al., 2022; Morrill et al., 2022; Pongrácz et al., 2007; Salomons et al., 2021) is a source of bias and hinders our understanding of dog behavioural ecology and evolution. Furthermore, the widely used terms “feral” and “stray” to describe free-living dogs imply that these are animals that have absconded from their proper place. However, since most dogs do not live in the pet niche this perspective should be reversed: it is the pet dogs who are anomalous for their intense, normatively captive, relationship with people.

Ultimately, the shortcomings outlined above undermine the dog as a versatile and resourceful model system for range of fields within ecology and evolution.

3 DOG BEHAVIOURAL ECOLOGY IN THE ANTHROPOGENIC NICHE

Free-ranging dog populations express substantial variation in their behavioural ecology. This variation is key to understanding dogs' great success in the rapidly developing human-dominated niche across various environmental gradients, including urbanization, climate and social structures. Below we review the existing literature within this context.

3.1 Pack Structure & Reproductive Behaviour

3.1.1 Pack structure

Free-ranging dogs live in semi-stable social groups of varying sizes consisting of multiple breeding individuals of each sex and juveniles (Italy: Bonanni et al., 2010a; USA: Daniels & Bekoff, 1989; Spain: Font, 1987; India: Pal, 2011). It was previously thought that free-ranging dog packs lacked any higher social organization (Boitani & Ciucci, 1995) similar to the age-graded linear dominance hierarchies seen in wolf family groups (Packard, 2003). However, across five free-ranging dog packs recently studied in central and southern Italy, it was found that dominance rank was positive associated with age, and that age was a better predictor of rank than body size (Bonanni et al., 2017). Linear dominance hierarchies based on age have also been observed in dog packs in West Bengal, India (Pal et al., 1998a). Both these studies found that physical aggression was rare within packs, and instead dominance was established by ritualized aggression (Bonanni et al., 2017; Pal et al., 1998a) or submissive reversal (Bonanni et al., 2017), suggesting a tolerant dominance style similar to wolves (Baan et al., 2014). Affiliative intra-pack relationships may also play an important role in group-level decisions for free-ranging dogs. While older, high-ranking individuals were found to take a

leadership role more often in relation to group departures in Italy (Bonanni et al., 2010b), this successful initiation of cohesive pack movement was dependent on affiliative relationships rather than dominance status within the pack.

Contrary to earlier claims (Boitani et al., 2007; Boitani & Ciucci, 1995), dogs within free-ranging packs can show high levels of kinship. Specifically, genotyping of dogs in Italy has demonstrated that packs are partially formed by the retention of adult offspring from previous generations (Natoli et al., 2021). These results are supported by observations of packs from India and the United States with known pedigrees (Daniels & Bekoff, 1989; Paul & Bhadra, 2018). Thus, to some extent, dog social groups resemble those of wolves. Modern wolf family groups are formed when older offspring remain with the natal pack to help raise their younger siblings before they themselves disperse to form their own packs (Jacobs & Ausband, 2019; Mech & Boitani, 2003; Packard, 2003). However, dog groups are not as ubiquitously interrelated as is observed in wolves (Lehman et al., 1992; Stenglein et al., 2011) because unrelated individuals are more readily accepted into the pack.

3.1.2 Mating system

Various mating systems have been reported in dogs with polygynandry being the most common (Pal, 2011). This has been confirmed by genome-wide single-nucleotide polymorphism genotyping (Natoli et al., 2021). However, as in wolves, social monogamy, where the same pair breeds over several years, does occur (Italy: Natoli et al., 2021; India: Pal, 2011). Furthermore, evidence from a study on dogs in Italy suggests that matings, even in a promiscuous system, might be based on affiliative relationships (Cafazzo et al., 2014).

3.1.3 Pup rearing

Female free-ranging dogs are commonly described to rear their pups without assistance from the father or other pack members (Boitani et al., 2007; Boitani & Ciucci, 1995). However, in India free-ranging dogs have been frequently observed to engage in cooperative pup-rearing such as allomaternal care (i.e., females providing nursing and food regurgitation to pups that are not their own, Pal, 2017; Pal et al., 2021), nursing by multi generations of females (Paul et al., 2014), and biparental care (e.g., food regurgitation and pup guarding by both parents, Pal, 2005, 2017; Paul & Bhadra, 2018). Although abundantly observed in free-ranging dog populations in India, this type of cooperative breeding behaviour has to date not been reported in populations in other countries. This may be because dogs in India are readily observed, whereas dogs in more rural areas, as in Italy, den away from human settlements (Boitani & Ciucci, 1995; Bonanni & Cafazzo, 2014), and avoid people (Boitani et al., 1995). Because cooperative breeding should be more pronounced in habitats with unpredictable food resources, we should expect to see variation in this behaviour across populations of free-ranging dogs. Additionally, as outlined above, free-ranging dogs adopt varying mating strategies. A minority form socially monogamous pairs, like wolves, where biparental care naturally follows. However, the generally polygynadrous mating-system of free-ranging dogs (Natoli et al., 2021; Pal, 2011), combined with the documented offspring retention and low dispersal distances (Natoli et al., 2021; Pal et al., 1998b, see below), will ultimately produce packs with high levels of relatedness. This could, in theory, increase the likelihood of cooperative breeding by kin selection (Hamilton, 1964). We therefore do not expect that cooperative breeding and/or paternal care are unique to the free-ranging dog populations of India.

3.2 ***Habitat Selection***

3.2.1 Home range size

Home range size varies dramatically across free-ranging dog populations. In rural, central Italy, Boitani et al. (1995) radio-collared members of a dog pack and reported an average home range of 11.7 km^2 over four years. The core areas of these home ranges were subject to change according to a number of factors, including human disturbance, wolf activity in the area, denning activities, the habitual space use and activity patterns of newly recruited pack members, and the unpredictability of food resources. In densely populated areas in West Bengal, India, Pal et al. (1998b), reported mean home range sizes up to two orders of magnitude smaller than in Italy (0.052– 0.116 km^2). These highly variable home range sizes across dog populations can likely be explained by a combination of factors affecting home range size in other species (Macdonald, 1983). Free-ranging dog populations in less populated areas (e.g., Italy) rely on more unpredictable food resources than populations in densely populated environments (e.g., India), where scavenging opportunities are abundant. Additionally, the pack studied in rural Italy was twice the size (11 dogs, Boitani et al., 1995) of the urban packs studied in West Bengal (mean = 5.5 dogs, Pal, 2017). This difference in pack size associated with levels of urbanization is confirmed in other studies, where packs studied in less urbanized areas in Italy ranged in size from 3 to 27 individuals (mean = 15, Natoli et al., 2021), and three additional packs from heavily urbanized areas in West Bengal, India, averaged 6.5 dogs per pack (Bhattacharjee & Bhadra, 2020).

3.2.2 Space use, movement and activity budgets

Space use and activity budgets are subject to great variation across free-ranging dog populations. For example, dogs in rural Italy actively avoid human food resources such as dump sites during human activity hours (Boitani et al., 1995), whereas the activity of urban-

living dogs in India coincides with human activity (Banerjee & Bhadra, 2022). In comparison, wolves generally avoid human settlements and structures (Carricondo-Sanchez et al., 2020; Ciucci et al., 1997) leading to nocturnal activity budgets (Ciucci et al., 1997). Thus, while free-ranging dogs in rural areas seem to adopt similar behavioural strategies to wolves when it comes to general space use, dogs living in densely populated areas express very different behavioural patterns.

In both Italy and India free-ranging dogs are reported to disperse over only modest distances. In a study of 64 litters in West Bengal, India, the average dispersal distance for juvenile dogs was only 1.7 km with no difference between males and females (Pal et al., 1998b). In spite of the large differences in home range sizes between dogs in India and Italy, dispersal distances of dogs in Italy are also relatively small, with individuals primarily dispersing to neighbouring packs (Natoli et al., 2021). Based on genetic sampling, the results from the Italian study, demonstrated how short-distance dispersal can create a kinship network between neighbouring packs, which suggests that free-ranging dogs within the same area could be more related than previously thought.

3.2.3 Denning sites

Pregnant dogs in India prefer to den in urbanized areas (Majumder et al., 2016). In Italy, female dogs den in close proximity to the group's core home range areas, which are often not close to human settlements (Boitani et al., 1995). This variation in denning sites likely reflects general differences in home range sizes, and the costs and benefits associated with proximity to human settlements. All these factors can be influenced by human cultural attitudes towards dogs. While pups in densely human-populated areas suffer high human-caused mortality (e.g.,

vehicle collisions, human interference, Pal, 2001), proximity to humans also provides easy access to food resources (Boitani & Ciucci, 1995), which can increase pup survival.

3.2.4 Territorial defence

Free-ranging dog groups have been widely reported to engage in cooperative territorial defence at multiple sites (Italy: Boitani et al., 2007; Bonanni et al., 2010a, 2010c; Spain: Font, 1987; India: Pal, 2015, 1998a; USA: Daniels & Bekoff, 1989), for instance by marking (Bonanni et al., 2010c; Pal et al., 1998a) and barking (Bonanni et al., 2010c; Daniels & Bekoff, 1989; Pal, 2015). Additionally, detailed studies in Italy have demonstrated that dogs use complex agonistic group-level behavioural displays to cooperatively defend their territory during intergroup conflicts (Bonanni et al., 2010c). In these conflicts, dogs assess the relative size of opposing groups before engaging in aggressive encounters. However, intragroup cooperation is not equally distributed. The proportion of total cooperation within a group during intergroup conflicts (measured as active engagement in agonistic behavioural displays towards the opposing group) decreases with group size so that dogs in smaller groups are more cooperative than dogs in larger ones (Bonanni et al., 2010a). Furthermore, the number of affiliative partners a dog has within a group is positively associated with its likelihood to cooperate during intergroup conflicts.

3.3 Foraging

Free-ranging dogs are opportunistic foragers. As outlined in section 1.2, the majority of free-ranging dogs are scavengers, mainly on human refuse (Coppinger & Coppinger, 2001; Sarkar et al., 2019) but also on carcasses (Boitani et al., 1995). Hunting is rarely observed, but does occur (Butler et al., 2004; Duarte et al., 2016; Silva-Rodríguez & Sieving, 2012). While

334 remains of various wildlife species are commonly found in dog scat (e.g., deer in Wisconsin:
335 Bergeron & Pierre, 1981; coati in Brazil: Campos et al., 2007) it is unclear whether these food
336 resources were obtained via scavenging or hunting, and how common hunting is in dogs.
337 Hunting behaviour in free-ranging dogs has been reported in various locations (Zimbabwe:
338 Butler et al., 2004; Spain: Duarte et al., 2016; Chile: Silva-Rodríguez & Sieving, 2012).
339 However, the success of hunting as a foraging strategy among dog populations varies
340 dramatically. For instance, in Zimbabwe only 20 kills were recorded in a year-long survey of
341 236 dogs (Butler et al., 2004). The lack of hunting success was explained by a range of
342 parameters, including small pack size (mean = 1.7), low body weight of dogs (mean = 14.7 kg)
343 likely preventing the successful take down of larger prey, abundant scavenging resources in
344 the area, and a large fraction of juvenile, inexperienced dogs in the population. In a study from
345 Spain, a single pack of 3-5 adult dogs depredated 57 small to medium-sized ungulates in only
346 six months (confirmed predations where dogs were the only carnivores in the area, Duarte et
347 al., 2016). This highly efficient foraging strategy was explained by the larger body mass of the
348 dogs in this study (estimated mean = 25 kg), and the fact that they did not have access to human
349 refuse as a scavenging option. Additionally, the Spanish dogs selected fawns and females
350 among the medium-sized ungulates but did not discriminate in their choice of prey among
351 smaller sized ungulates. This preference for smaller prey is also seen in wolves (Smith et al.,
352 2004).

353

354 The only *in situ* experiments on foraging strategies have all been carried out in West Bengal,
355 India. Here dogs have been observed foraging both individually and in groups (Majumder et
356 al., 2013). When foraging individually, dogs seek to maximise both the quality and quantity of
357 food sources (Sarkar et al., 2019), but at the cost of increased vigilance behaviour
358 (Bhattacharjee et al., 2020). In groups, dogs show less selectivity of food resources and reduced

359 vigilance, leading to more efficient exploitation of food patches (Bhattacharjee et al., 2020). In
360 another foraging experiment in Pune, India, male dogs as well as pregnant and lactating females
361 were more efficient and sophisticated foragers than non-reproductive females when presented
362 with novel, experimental food packets (Mangalam & Singh, 2013). Non-reproductive females
363 compensated for their less efficient foraging by actively food guarding. These results likely
364 reflect a combination of variations in motivational state, and males' and reproductive females'
365 higher energy requirements (Mangalam & Singh, 2013).

366

367 ***3.4 Cooperation***

368 *3.4.1 Conspecific cooperation*

369 Although the evidence from territorial defence indicates cooperative activity, experimental
370 studies have so far been unable to demonstrate conspecific cooperation in dogs. To date, there
371 have been no controlled studies of cooperation in free-ranging dogs, but some insights can be
372 gained from research on dogs living in conspecific groups in captive settings, some which
373 include direct comparisons with similarly-raised wolves. In a test of dogs' and wolves'
374 readiness to cooperate, Range et al. (2015) offered a potentially monopolizable food item to
375 pairs of dogs and pairs of wolves. They found that in each pair the dominant wolf, but not the
376 dominant dog, tolerated feeding by the subordinate individual. Similarly, Dale et al. (2017)
377 using study subjects from the same populations, reported that pairs of wolves, but not dogs,
378 shared a carcass. In each study, subordinate dogs, unlike subordinate wolves, were almost
379 entirely prevented from feeding by the dominant individual in each pair. Marshall-Pescini et
380 al. (2017) also tested these populations of dogs and wolves on a string-pulling task which
381 required two individuals to pull simultaneously, each on one end of a string, for either of them
382 to receive a food reward. Although levels of engagement with the task were similar in the two

383 species, only the wolves successfully cooperated and obtained the available food. This
384 difference between wolves and dogs, and between dogs in these experiments seeking food and
385 free-ranging dogs practicing territorial defence, may be because food sought by dogs is often
386 distributed in quantities that are small enough to be monopolised by individuals (Sarkar et al.,
387 2019) and sufficiently easy to recover that cooperation with conspecifics would not be helpful.

388

389 *3.4.2 Interactions with humans*

390 Success in anthropogenic environments must to a large extent be driven by tolerance of human
391 proximity. Free-ranging dogs express high levels of variation in their reaction towards people
392 across populations.

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394 In Kolkata, India, interspecific interactions with humans make up a larger proportion of social
395 interactions than intraspecific interactions with other dogs (Bhattacharjee & Bhadra, 2020).
396 Evidence from Italy (Boitani et al., 1995) suggests an environment in which dogs encounter
397 humans at a much lower rate, but unfortunately, comparable data on rates of interaction are not
398 available from outside India. However, we note that dogs in Italy are reported to avoid hours
399 of human activity (Boitani et al. 1995). Bhattacharjee et al. (2021) compared human-directed
400 sociability of dogs living in urban zones with different levels of human movement. Dogs in the
401 zone with the least human movement showed the lowest levels of sociability towards humans.
402 These effects would be predicted to be stronger when comparing urban and rural populations
403 but no such study has been reported.

404

405 In India, free-ranging dogs experience high levels of persecution from humans, but at the same
406 time rely on humans for survival, sometimes by begging for food (Bhattacharjee et al., 2017).

This creates a landscape where dogs must constantly assess the intentions of unfamiliar people. Bhattacharjee et al. (2017) reported that free-ranging dogs in Kolkata were initially wary of unfamiliar people, but given a choice in a long-term exposure test between a person with a friendly disposition and a piece of chicken they choose social contact over food. This indicates that affiliative relationships might also play a significant role in dog-human relationships.

In Morocco, *in situ* experiments have shown that free-ranging dogs adopt novel foraging strategies based on the observed behaviour of an unfamiliar human demonstrator (Cimarelli et al., 2023). Specifically, two groups of dogs were exposed two novel foraging boxes each containing a food reward. One group of dogs was allowed to observe an unfamiliar human forage from one of the boxes before they themselves were given the opportunity to utilize the new foraging source. The other dog group received no demonstration. Dogs that had observed a human demonstrator matched their box choice to that of the human, whereas the dogs that had not received a demonstration chose between the two boxes at random. This experiment suggests that dogs can engage in interspecific social learning (Cimarelli et al., 2023), which for free-ranging dogs living as scavengers on human refuse in urban environments likely will be highly beneficial.

3.4.3 Cooperation with humans

Dogs' readiness to cooperate with humans in a range of domains, from hunting to guide dogs for the blind is often remarked upon (Bray et al., 2021; Salomons et al., 2021), but the literature lacks any studies on cooperation between free-ranging dogs and humans.

The most closely related studies were carried out on similarly-hand-reared wolves and dogs using the string-pulling task described above. Range et al. (2019) 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 above chance. However, in a complete analysis, the species effect was not significant. Interestingly, wolves and dogs adopted different strategies on the task, with wolves more inclined to take the lead in selecting a string to pull, whereas dogs were more likely to follow the human partner's lead. Given the large difference in 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 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. (2019) 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 (Duranton & Gaunet, 2018; Hare et al., 2002; Hare & Tomasello, 2005; Kaminski, 2021; Salomons et al., 2021; Topál et al., 2005, 2009) and more studies are needed to clarify the conditions under which dogs and wolves may cooperate with people.

5. CONCLUDING REMARKS AND FUTURE DIRECTIONS

In this review we have sought to recontextualize the dog as a study species. Much current research on dog behaviour views dogs as products of human intention with human-like cognitive capacities, possibly unique in the animal kingdom (see Buttner, 2016; Duranton & Gaunet, 2018; Hare et al., 2002; Hare & Tomasello, 2005; Topál et al., 2009). Contrary to this

454 highly anthropomorphic view, we argue that, while thoroughly integrated into human-
455 dominated environments, the dog has a well-defined species ecology in three distinct niches:
456 pet, scavenger and hunter, of which the pet niche only amounts to approximately 20% of the
457 global dog population. Furthermore, although, on our estimates, 90% of the global dog
458 population is subject to natural selection through uncontrolled breeding, most research has been
459 carried out on the minority of dogs subject to artificial selection in the pet niche and much less
460 on dogs in the scavenger and hunter niches.

461

462 Studies on free-ranging dog behavioural ecology are sparse, and the ones that exist are limited
463 primarily to sites in India and Italy. This narrow range of locations, combined with a lack of
464 standardization across studies and limited knowledge of the history of populations studied,
465 makes comparisons challenging. To move the field forward we suggest studies on free-ranging
466 dogs at more locations, with a coordinated effort to standardize protocols and designs across
467 global study sites for large-scale comparisons. The limited research on free-ranging dogs is
468 particularly disappointing because the highly heterogenic environments in which dogs live on
469 a global scale, combined with our in-depth knowledge of their evolutionary history, the
470 advanced genetic tools specifically developed using dogs (Dutrow et al., 2022; Morrill et al.,
471 2022; Parker et al., 2017; vonHoldt et al., 2010) offer a unique set of advantages for
472 comparisons across populations.

473

474 The many advantages of the dog highlight the strength and value of this species' potential as a
475 model for a range of fields. Specifically, dogs provides an opportunity to collect comparable
476 data across different climatic zones, social groupings, and levels of urbanization, where diverse
477 behavioural ecologies can be found within one species. Studies like this could be of great value

especially to urban ecology and evolution. Winchell et al. (2023) identified three classes of animals found in urban environments: *urban adapters, urban avoiders*, and *urban exploiters* (where "adapter" is being used in the absence of proof of trait heritability). As outlined above, free-ranging dog populations are encountered in all three contexts: As *urban adapters* in environments where they rely on both anthropogenic and non-anthropogenic resources (Bhattacharjee et al., 2017; Butler et al., 2004; Mangalam & Singh, 2013) ; As *urban exploiters* where they rely heavily on non-anthropogenic resources (Duarte et al., 2016); as well as populations that live as *urban avoiders* (Boitani et al., 1995).

Furthermore, the research reviewed here demonstrates that, while present-day dog behaviour is well suited to anthropogenic environments, these behaviours can also be observed, albeit at lower frequencies, in wolves. It is therefore likely that many dog behaviours have evolved from standing variation in ancestral wolf populations. Similarly, it seems highly likely that the behaviours that differ between wolves and dogs and between different populations of dogs constitute a component of dogs' adaptations to human-dominated environments. However, in the absence of any research on the heritability of these behaviours, this can only constitute plausible speculation. We therefore encourage studies on the heritability of dog behaviours with documented variation across populations to clarify which behavioural differences are indeed adaptations.

Finally, studies on free-ranging dogs will also help advance our understanding of the behaviour of dogs in the pet niche. These dogs have enormous economic and emotional significance to hundreds of millions of people. Ongoing attempts to understand the underlying mechanisms of dog behaviour, which are central to dog training and other aspects of human-pet dog

interaction, are grossly limited when the animals are not free to express species-typical behaviours but are rather continuously buffered by human intervention in their lives.

In sum, this review has sought to highlight how a range of misconceptions and biases surrounding the dog as a species hinders the study of its behaviour, and how free-ranging dogs can provide an outstanding model for the study of urban ecology and evolution.

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