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

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 reviewing the available literature on free-ranging dog behavioural ecology we place the dog within an objective biological framework. We find that free-ranging dog populations express substantial variation in their behavioural ecology across their global range and propose that this variation 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 in-depth knowledge of dog evolutionary history and the advanced genetic tools specifically developed using this 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* (J. P. 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 as 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 dog populations, and 2) understanding how this variation could have arisen. 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, drawing on examples from the free-ranging dog population. This illustrates 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 address 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; Zeder, 2012) that the process was initiated when some ancestral wolves with reduced fear associated themselves as commensals within the new niche created by humans (Boitani & Ciucci, 1995; Larson & Fuller, 2014). These less fearful wolves exapted (Gould & Vrba, 1982; Winchell et al., 2023) to human proximity were able to exploit a new food resource by scavenging on human refuse, and thereby represent the first known example of exaptation to an anthropogenic niche. As these wolves adapted further to the human niche, some of their behaviours were initially serendipitously advantageous to their human hosts. These likely included alarm and guard functions as well as aiding hunters as the climate warmed and landscapes became more dense and difficult for human hunters to navigate (Perri, 2016).

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

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

In the Western world, dogs are mostly viewed as pets: an animal defined by being owned by a person for whom it serves no function beyond companionship (Tague, 2017). Estimates vary, but of the global dog population of around a billion individuals (Gompper, 2014), only 17-24% can be categorized as pets, restricted to households (Hughes & Macdonald, 2013; Lord et al., 2013). Categorizing the approximately 80% of non-pet dogs is complex. In different parts of the world, people may see themselves as having an emotional bond with dogs they do not consider their property (Coppinger & Coppinger, 2001), or may consider dogs to be their property without acknowledging any emotional connection to them (Coppinger & Coppinger, 2016). Human notions of ownership may also interact partially, if at all, with ecologically relevant behaviours such as foraging and reproduction. Even when considered someone's property or receiving food from people these dogs are free-ranging and thus forage and reproduce with little human interference. Free-ranging dogs exist along multiple continua, of which the most important for their impact on other species is foraging strategy. Independent of whether people view them as owned or not, free-ranging dogs scavenge and hunt. The majority of free-ranging dogs are scavengers (Coppinger & Feinstein, 2015). Dogs may scavenge even if they are provisioned food by their owners (Muinde et al., 2021), or are occasionally intentionally provisioned by humans, and unowned dogs who live in proximity to humans generally 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). Some dogs hunt, but with highly variable success (Butler et al., 2004; Duarte et al., 2016), and only a few populations likely subsists as true hunters, not reliant on human-originating food sources (Coppinger & Coppinger, 2001; Duarte et al., 2016; Macdonald & Carr, 2016). Dogs may transition between pet and free-ranging, as pets may be abandoned. These dogs are most likely to become scavengers (Makenov & Bekova, 2016). Similarly, free-ranging dogs may be adopted into human homes as pets (Coppinger & Coppinger, 2001).

McKinney (2006) identified three classes of animals found in urban environments: *urban adapters, avoiders*, and *exploiters* (where "adapter" is being used in the absence of evidence of trait heritability). Based on these groupings it is clear that free-ranging dog are encountered in all three contexts: As *urban adapters* in environments where they rely on both anthropogenic and non-anthropogenic resources (*sensu* Winchell et al., 2023, e.g. Bhattacharjee et al., 2017; Butler et al., 2004; Mangalam & Singh, 2013); As *urban exploiters* where they rely heavily on non-anthropogenic resources (*sensu* Winchell et al., 2023, e.g. Duarte et al., 2016); as well as populations that live as *urban avoiders* in rural habitats (Boitani et al., 1995).

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). Comparable data do not appear to be available for other territories, but since the United States has a relatively high rate of sterilization of dogs (70%, Clancy & Rowan, 2003), it is a reasonable assumption that this represents a relatively high level of human control over pet dog reproduction. Humans also exert artificial selection over free-ranging dogs via neutering campaigns, and human action is major cause of mortality in free-ranging dogs (e.g. culling, traffic collisions: Boitani et al., 1995; Coppinger & Feinstein, 2015; D. Macdonald & Carr, 2016; Pal, 2005). However, as human intervention on free-ranging dog reproduction is unsystematic and population turnover rates are generally high, these effects are minimal on a global scale (Evans et al., 2022; Gompper, 2014; Taylor et al., 2017). In sum, only approximately 50% pet dog matings are under human control, and the proportion of free-roaming dog matings affected by humans is likely to be close to zero. This then implies that world-wide only around 10% (i.e., 50% of the approximately 20% of dogs that live as pets) of dog matings are the outcome of artificial selection. Subsequently, 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 (see e.g., for reviews, Bensky et al., 2013; Lea & Osthaus, 2018) is a source of bias and hinders our understanding of dog behavioural ecology and evolution. Aria et al., 2020, using a co-occurrence analysis of keywords identified four thematic clusters in papers referring to dogs published from 2006 to 2018. While this analysis revealed that the interest in dog research has increased sharply during the study period, none of these themes related to free-ranging dogs.

The widely used terms “feral” and “stray” to describe dogs that are not pets 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. In order to avoid unsubstantiated assumptions, we refer to dogs that are not restricted to human domiciles simply as "free-ranging." In some cases, these dogs may be perceived as the property of certain people, and where this is reported we note it appropriately. Many studies, however, do not include data on whether the dogs they observed were owned or not.

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, occupying roles as urban adapters, exploiters or avoiders (*sensu* McKinney, 2006; Winchell et al., 2023). This variation is key to understanding dogs' great success in the human-dominated niche across various environmental gradients, including urbanization, climate and social structures. Below we review the available literature within this context for social, reproductive, spatial, and foraging ecology, and behaviour expressed towards humans.

3.1 Social ecology

3.1.1 Pack structure

Free-ranging dogs live in semi-stable social groups of varying sizes (Table 1) consisting of multiple breeding individuals and juveniles (Bonanni et al., 2010a; Daniels & Bekoff, 1989; Font, 1987; Pal, 2011). Contrary to earlier claims (Boitani et al., 2007a; Boitani & Ciucci, 1995), some free-ranging packs express high levels of kinship. Specifically, genotyping of free-ranging 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). Retention of offspring in other species is commonly associated with habitat saturation, cost of dispersal, or habitat quality (Emlen, 1982), and it seems likely that similar factors play a role in the social ecology of free-ranging dogs. As we mention below under Spatial Ecology, dispersal distances in free-ranging dogs are generally low, which can further contribute to kin structure within packs. However, the extent to which packs are made up of kin individuals as well as whether this social structure is affected by ecological factors such as habitat and climate across dogs' global distribution is currently unknown due to the lack of relevant studies.

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 positively 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.

Studies of social behaviour in owned free-ranging dogs are sparse and mainly focus on social networks with the purpose of modelling zoonotic disease risk (e.g. rabies). A handful of studies has provided some insights on contact networks in owned free-ranging dogs in Chad, Guatemala, Indonesia, Uganda, and Australia, where it has been demonstrated that interconnectedness between individual dogs is high (Brookes et al., 2020; Laager et al., 2018; Warembourg, Fournié, et al., 2021; Wilson-Aggarwal et al., 2019). These studies have also revealed that dogs from households in closer proximity are more likely to be in contact (Warembourg, Fournié, et al., 2021; Wilson-Aggarwal et al., 2019), and dogs in rural areas are more connected than dogs in urban areas (Warembourg, Fournié, et al., 2021). However, notwithstanding these studies, we currently know very little about the general social ecology of this dog group. This includes questions regarding temporary pack formation, dominance dynamics, and affiliative relationships, and how these social constructs in turn might vary across populations or affect other behavioural ecologies.

3.1.2 Reproductive ecology

Various mating systems have been reported in dogs, including polygyny, polyandry, polygynandry and promiscuity (Pal, 2005, 2011, Natoli et al., 2021). Genome-wide single-nucleotide polymorphism genotyping has confirmed that polygynandry is the most common mating system in an Italian population of free-ranging dogs (Natoli et al., 2021). However, as commonly seen in the Canidae family (Macdonald et al., 2019), social monogamy, where the same pair breeds over several years, has been observed in both Italy (Natoli et al., 2021) and 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). This great behavioural plasticity in mating systems across dog populations presents an excellent opportunity to study how environmental factors affect reproductive strategies on a large scale within the same species. While it has been proposed that readily available anthropogenic food resources have led to selection for the loss of biparental care and reproductive seasonality in dogs (Lord et al., 2013), far from all dogs have reliable access to food, even in urban habitats. Additionally, monogamy does occur in dogs (Natoli et al., 2021; Pal, 2011), and as detailed below, biparental care may be more common than previously thought (Pal, 2005, 2017; Paul & Bhadra, 2018). Therefore, though environmental factors undoubtedly have a substantial effect on present-day dog mating strategies, these factors are likely highly complex and need to be adequately disentangled.

Female free-ranging dogs are commonly described to rear their pups without assistance from the father or other pack members (Boitani et al., 2007a; 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). Additionally, as outlined above, free-ranging dogs adopt varying mating strategies. A minority form socially monogamous pairs, like many other canid species (Macdonald et al., 2019), 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. Furthermore, because cooperative breeding should also be more pronounced in habitats with unpredictable food resources, the extent of cooperative breeding may be subject to significant variation across dog populations as a result of interactions between kin relationships within packs and availability of food resources. For instance, anthropogenic food resources likely vary even within urban habitats, and some rural populations might experience large fluctuations in prey availability. In some canid species, including wolves and African wild dogs (*Lycaon pictus*), helpers only contribute to feeding pups if food is abundant (Harrington et al., 1983; Malcolm & Marten, 1982). More studies are needed to disentangle the potential genetic and ecological factors driving this social behaviour in dogs.

3.1.1 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.

3.2 ***Spatial ecology***

3.2.1 Home range size

Home range size varies dramatically across free-ranging dog populations worldwide (Table 1). Studies report home range sizes from 8.4 ha in urban India to 1170 ha in rural Italy (Boitani et al., 1995; Pal et al., 1998b). Individual free-ranging dogs in Brazil have home range sizes as small as 0.0048 ha (Melo et al., 2020), whereas individuals in rural Puerto Rico have been found to have home ranges up to 108 ha (Sauvé et al., 2023). Home range size for individual owned free-ranging dogs have been reported to vary from 5.6 ha in rural to semi-urban Indonesia (Warembourg, Wera, et al., 2021) to 350 ha in rural Chile (Schüttler et al., 2022). Common for these studies (Table 1) is that home ranges sizes are subject to substantial individual variation within dog populations, with some dogs having very small or very large home ranges. While this variation in some instances can be related to age, sex, and/or reproductive status (Dürr et al., 2017; Warembourg, Wera, et al., 2021), several abiotic factors can significantly influence home range size. Free-ranging dog populations in less populated areas (e.g., Italy, United States) rely on more unpredictable food resources than populations in densely populated environments (e.g., India, Brazil), where scavenging opportunities are abundant, which can lead to larger home range sizes. Similarly, while some owned free-ranging dogs spend time at dump sites (Muinde et al., 2021), this group must be assumed to receive at least some food resources from their owners (Schüttler et al., 2022; Warembourg, Wera, et al., 2021), thereby reducing their need for roaming to forage. This could explain why owned free-ranging dogs are often found in or near their household or village (Muinde et al., 2021; Pérez et al., 2018; Vanak & Gompper, 2010; Wilson-Aggarwal et al., 2021). Home range size in this dog group is therefore likely affected by factors that are likely highly individual and dependent on the demography and habits of their owners (Warembourg, Wera, et al., 2021; Wilson-Aggarwal et al., 2021). Lastly, for both owned and un-owned free-ranging dogs, home range size is likely to change due to human disturbance, predator presence, season, or newly discovered food resources (Boitani et al., 2007b; Carvalho et al., 2019; Pal et al., 1998b; Wilson-Aggarwal et al., 2021).

Table 1. Summary of spatial ecology metrics for free-ranging dogs across the world. *The following parameters are listed: Country with specified study site, free-ranging dog type sampled, habitat in which the study was performed, number of individual dogs (N) sampled with pack sizes given when whole free-ranging packs were studied (note that for countries where multiple references are given N is referring to the study used to obtain home range size), mean home rage size in ha with median home range size for a few studies were mean was not given, activity patterns of the dogs, habitat selection by the dogs, method used in the study, and reference.*

Country	Dog type	Habitat	N	Mean home range, ha	Activity pattern	Habitat selection	Method	Reference
Australia								
Northern Peninsula, Northern Territory	Owned	Rural	135	6.79	*NA*	*NA*	GPS collars	*(Dürr et al., 2017)*
Brazil								
Minas Gerais	Un-owned	Urban	270	0.0448	*NA*	Food outlets	Capture-recapture	*(Melo et al., 2020)*
Augusto Ruschi Biol Res	Un-owned, Owned	Rural	17	*NA*	Cathemeral	*NA*	Camera trapping	*(Zanin et al., 2019)*

Serra do Japi Biol Res	Un-owned (presumed)	Rural	*NA*	*NA*	Crepuscular	*NA*	Camera trapping	*(Carvalho et al., 2019)*
Cambodia								
Stung Treng	Owned	Rural	13	117.28	Nocturnal	*NA*	GPS collars, camera trapping	*(Ladd et al., 2023)*
Chad								
Guelendeng, Sarh	Owned	Rural	174	42.5 (median)	Diurnal, Nocturnal	Household, village	GPS collars	*(Wilson-Aggarwal et al., 2021)*
Moyen-Chari, Batha	Owned	Rural	106	7.7	*NA*	*NA*	GPS contact sensors	*(Warembourg, Wera, et al., 2021)*
Chile								
Navarino Island	Owned	Rural	41	350	Diurnal, Nocturnal	Forest, infrastructure, coast	GPS collars	*(Schüttler et al., 2022)*
Puerto Natales	Owned	Urban	86	65	Diurnal	Infrastructure, households	GPS collars	*(Pérez et al., 2018)*
Ethiopia								
Bale Mountains Natl Park	Owned	Rural	119	*NA*	Diurnal	Grassland	Observations	*(Perry et al., 2018)*
Guatemala								
Petén dept	Owned	Rural, Urban	303 (HR)	5.7	Crepuscular	Roads, buildings	GPS contact sensors, FitBark tracker	*(Cunha Silva et al., 2022; Griss et al., 2021; Warembourg, Wera, et al., 2021)*
India								
West Bengal	Un-owned	Urban	5.5 (pack size)	8.4	*NA*	*NA*	Observations	*(Pal, 2017; Pal et al., 1998b)*
Great Indian Bustard Sanctuary	Un-owned, Owned	Semi-urban	25	45	*NA*	Human settlements, agricultural land, bare-ground	GPS collars	*(Vanak & Gompper, 2010)*
Indonesia								

Flores Island	Owned	Rural, Semi-urban	217 (HR)	5.6	Crepuscular	Roads, buildings	GPS contact sensors, FitBark tracker	*(Cunha Silva et al., 2022; Griss et al., 2021; Warembourg, Wera, et al., 2021)*
Italy								
Abruzzo	Un-owned	Rural	11 (pack size)	1170	Crepuscular	Woodland, praire, ruins, dump sites	Radio-collars. Observations	*(Boitani et al., 1995)*
Kenya								
Busia county	Owned	Rural	29	12.34 (median)	*NA*	Household, fields, dump sites	GPS collars	*(Muinde et al., 2021)*
Busia county	Owned	Urban	44	8.14 (median)	*NA*	Household, fields, dump sites	GPS collars	*(Muinde et al., 2021)*
Puerto Rico								
Jobos Bay Natl Estuarine Research Res	Un-owned	Rural	5	108	*NA*	*NA*	GPS collars	(Sauvé et al., 2023)
Russia								
Karelia	Un-owned	Urban	*NA*	36.2	*NA*	*NA*	Observations	*(Ivanter & Sedova, 2008)*
Uganda								
Soroti	Owned	Rural, Semi-urban	149	5.7	*NA*	*NA*	GPS contact sensors	*(Warembourg, Wera, et al., 2021)*
United States								
Alabama	Un-owned	Rural	2 - 5 (pack size)	686.33	Nocturnal	Flood plains, dry upland	Radio-collars. Observations	*(M. D. Scott & Causey, 1973)*
Arizona	Un-owned	Rural	9 (pack size)	88	Crepuscular	Dump site	Radio-collars. Observations	*(Daniels & Bekoff, 1989)*
Arizona	Un-owned	Rural	3 (pack size)	19	Crepuscular	Dump site	Radio-collars. Observations	*(Daniels & Bekoff, 1989)*

3.2.2 Activity patterns and habitat selection

As for home range size, free-ranging dogs display great variation in activity patterns and habitat selection. Across their distribution dogs have been reported to adopt diurnal, nocturnal, crepuscular and cathemeral activity patterns (Table 1). This large variation in activity patterns is likely an expression of local adaptation to a range of factors, such as climate (Wilson-Aggarwal et al., 2021), foraging routines (Boitani et al., 1995; Daniels & Bekoff, 1989), prey activity (Carvalho et al., 2019), predator avoidance (Carvalho et al., 2019), synchronization with human activity (Banerjee & Bhadra, 2022; Boitani et al., 1995), and, for owned dogs, owner routines and activities (Wilson-Aggarwal et al., 2021). For example, un-owned 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). While such activity patterns are likely driven by fear of people in dogs in rural settings (urban avoiders) and a reliance on begging for food in dogs in urban settings (Bhattacharjee et al., 2017), even urban-adapted dogs are sensitive to sudden changes in their environment. This has been demonstrated in India, where an abrupt surge in human activity in association with a festival caused a temporal displacement of a local, urban free-ranging dog population, with a significant decrease in their daily activity patterns (Bhattacharjee & Bhadra, 2021).

Studies on habitat selection in free-ranging dogs are sparse (Table 1). While drawing general conclusions based on these studies is challenging, as they are inevitably confounded by the study sites in which they were conducted (e.g. urban dogs cannot select woodland habitat like rural dogs), some potentially valuable observations can be made. Owned dogs often select habitat containing infrastructure, including buildings and roads (Table 1), yet such human-made features can also influence their movement. In Chad (Laager et al., 2018), network analyses demonstrated that contact between communities of urban owned dogs was restricted by roads with high-intensity traffic. Similarly, in rural Italy, the core home range areas of un-owned dogs have a lower density of roads than more peripheral areas, indicating a general avoidance of roads (Boitani et al., 1995). It is therefore possible that infrastructure plays a significant role in habitat selection for dogs in general, regardless of the habitat they live in or their ownership status.

Lastly, pregnant dogs in urban India prefer to den in areas with high human activity (Majumder et al., 2016). In rural 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 between urban and rural dog populations, but also the costs and benefits associated with proximity to human settlements. Hence, while pups in densely human-populated areas suffer high human-caused mortality (e.g., vehicle collisions, human interference, Pal, 2001), proximity to humans can also provide easy access to food resources for the female and increase pup survival (Majumder et al., 2016, Boitani & Ciucci, 1995).

3.2.3 Dispersal

The few available studies on dispersal in free-ranging dogs have found generally modest dispersal distances. In a study of 64 litters in West Bengal, India, the average dispersal distance for juvenile free-ranging dogs was only 1.7 km with no difference between males and females (Pal et al., 1998b). While low dispersal distance could be expected in densely populated areas, free-ranging dogs in a nature reserve near Rome, Italy, also disperse over relatively small distances, and usually to neighbouring packs (Natoli et al., 2021). Using genetic sampling, the Italian study further demonstrated how short-distance dispersal can create a kinship network between neighbouring packs. This suggests that free-ranging dogs within the same area could be more related than previously thought, which should be taken into account for future population level studies. However, due to the lack of additional studies on dispersal in free-ranging dogs it is currently unknown if dogs in general express short dispersal distances. Thus, while studies have found that individual owned free-ranging dogs roam as far as 20.4 km from their household in Chile (Schüttler et al., 2022), and travel average distances of 10.9 and 13.5 km daily in Cambodia and Kenya, respectively (Ladd et al., 2023; Muinde et al., 2021), it remains unclear why actual dispersal distances are so much lower than widely reported roaming distances. One potential explanation for short dispersal distances is that long-distance dispersal in dogs could be costly and associated with negative fitness consequences. Since most dog populations have promiscuous mating systems (Natoli et al., 2021; Pal, 2011), individual dogs are not reproductively constrained by staying in, or close to, their natal habitat. The costs of long-distance dispersal could therefore outweigh the cost of staying in the area as it might be difficult to find other suitable habitat due to high population density. Dispersal might be also be associated with increased mortality risk due to roads with high traffic (Laager et al., 2018), or increased predation risk.

3.3 Foraging ecology

Free-ranging dogs are opportunistic foragers, and even owned dogs, though commonly fed by at least one household (Schüttler et al., 2022), engage in both scavenging and hunting activities. As outlined in section 2.2, the majority of dogs are scavengers, mainly on human refuse (Coppinger & Coppinger, 2001; Sarkar et al., 2019) but also on carcasses (Boitani et al., 1995). Hunting is scarce, but does occur (Butler et al., 2004; Duarte et al., 2016; Silva-Rodríguez & Sieving, 2012). While remains of various wildlife species are commonly found in dog scat (e.g., deer in Wisconsin: Bergeron & Pierre, 1981; coati in Brazil: Campos et al., 2007) it is unclear whether these food resources are obtained via scavenging or hunting, and thus how common hunting is in dogs. Hunting behaviour in free-ranging dogs has been reported in various locations (Zimbabwe: Butler et al., 2004; Spain: Duarte et al., 2016; Chile: Silva-Rodríguez & Sieving, 2012). However, the success of hunting as a foraging strategy among dog populations varies dramatically. In Zimbabwe 236 owned free-ranging dogs were recorded to only kill 20 prey within a year (Butler et al., 2004), whereas a single pack of 3-5 adult free-ranging dogs depredated 57 small to medium-sized ungulates in six months in Spain (Duarte et al., 2016). While motivational factors undoubtedly play a significant role in differences in hunting success between owned and un-owned free-ranging dog populations since owned free-ranging dogs are fed by their owners, a range of other factors likely also affects hunting success in dogs. For instance, some un-owned dog populations may not have access to scavenging resources, making hunting their only means of survival (Duarte et al., 2016). Yet, developing successful hunting techniques is highly dependent on pack cooperation and cohesion, efficient recruitment of juvenile pack members, and adjustment to the prey species in the habitat (Butler et al., 2004, Duarte et al., 2016). Though sparsely observed and studied, hunting behaviour is therefore likely to vary widely across free-ranging dog populations. Notably, some dog populations have been reported to engage in advanced hunting strategies, selecting fawns and females among medium-sized ungulates but not discriminating in their choice of prey among smaller sized ungulates (Duarte et al., 2016). This preference for smaller prey, which is also seen in wolves (Smith et al., 2004), is likely a strategy to save energy and reduce risk of injury (Schoener, 1971).

The only *in situ* experiments on foraging strategies have been carried out on scavenging free-ranging dogs in India. In Pune, in urban habitat, male dogs as well as pregnant and lactating females have been found to be more efficient and sophisticated foragers than non-reproductive females when presented with novel, experimental food packets (Mangalam & Singh, 2013). Non-reproductive females on the other hand, compensate for their less efficient foraging by actively food guarding. These results likely reflect a combination of variations in motivational state, and males' and reproductive females' higher energy requirements (Mangalam & Singh, 2013). In urban and semi-urban habitats in Western Bengal, dogs have been observed foraging both individually and in groups (Majumder et al., 2013). When foraging individually, dogs seek to maximise both the quality and quantity of food sources (Sarkar et al., 2019), but at the cost of increased vigilance behaviour (Bhattacharjee et al., 2020). In groups, dogs show less selectivity of food resources and reduced vigilance, leading to more efficient exploitation of food patches (Sarkar et al., 2019, Bhattacharjee et al., 2020). These observations align with optimal foraging strategies (Pyke et al., 1977; Schoener, 1971), with dogs expressing flexibility in foraging behaviour depending on context in order to maximize food intake (Sarkar et al., 2019). However, foraging strategies are likely to vary across dog populations due to a range of factors including habitat, dog density, pack dynamics, predator presence, and food resources. Therefore, more studies on a wider, comparable scale are needed to understand how foraging affects fitness in dogs.

3.4 Human-directed Behaviour

Success in anthropogenic environments must to a large extent be driven by tolerance of human proximity. Yet, besides the studies on habitat selection in anthropogenic environments, few studies have directly explored the behavioural expression of free-ranging dogs towards humans. However, valuable insights can be gained from the available studies.

Free-ranging dogs living in urban areas must be expected to encounter humans at significant higher rate than dogs in rural areas. Unfortunately, comparisons between dogs living in these different habitats are not possible as the majority of available studies on dog-human interactions come from heavily urbanized areas in India. Still, dogs in these urban areas vary in their sociability towards humans. Specifically, when dividing urban habitat into zones with varying levels of human movement, dogs in the zone with the least human movement expressed the lowest levels of sociability towards humans (Bhattacharjee et al., 2021). In Kolkata, interspecific interactions with humans made up a larger proportion of social interactions than intraspecific interactions with other dogs (Bhattacharjee & Bhadra, 2020). Under these conditions of intense exposure to human presence free-ranging dogs experience both high levels of persecution from humans, but at the same time rely on them 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. As an example, while dogs in Kolkata were initially wary of unfamiliar experimenter, when 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 (Bhattacharjee et al., 2017). In semi-urban settings in Ethiopia, owned free-ranging dogs overall fled when approached by an unfamiliar experimenter, while 11% expressed aggressive behaviour and 6% expressed friendly behaviour (Ortolani et al., 2009). Additionally, the social context the dog was in had a significant effect on the behavioural response, with dogs in groups being less likely to flee or displaying aggressive behaviour. While most free-ranging dogs in this study are presumed to be owned and therefore at least to some degree socialized, it may seem counterintuitive that only a minority of dogs expressed human-directed sociability. However, sociability towards strangers could be less important in owned free-ranging dogs because they are already fed at home. In contrast, for un-owned dogs in urban environments, as in India, affiliative relationships with people might have greater potential fitness consequences because food resources obtained directly from humans are more important for survival (Bhattacharjee et al., 2017). In line with this, *in situ* experiments in urban Morocco suggest that free-ranging dogs can engage in interspecific social learning (Cimarelli et al., 2023). Specifically, dogs were able to adopt novel foraging strategies based on the observed behaviour of an unfamiliar human demonstrator using a novel foraging box containing a food reward. The ability to exploit new resources through innovative learning could give dogs living as scavengers in close proximity to people a substantial fitness advantage.

In sum, even in urban environments, levels of urbanization and human presence create gradients affecting expression of human-directed social behaviour in dogs. While no good comparable data is available for rural populations, we note that free-ranging dogs in Italy are reported to avoid hours of human activity (Boitani et al., 1995), suggesting a fear of people. Although studies on human-directed sociability in free-ranging dogs are scarce, the available research indicates that this is a highly complex behaviour with many fine-scale interactions between habitat, food resources and exposure to humans in contexts where individual animals also learn from their life experiences.

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 highly anthropomorphic view, that focusses on the approximately 20% of the global dog population living as pets, we argue that, while thoroughly integrated into human-dominated environments, the dog has a well-defined species ecology.

Studies on the 80% of dogs that are free ranging remain sparse. The lack of standardization across studies and limited knowledge of the history of populations studied, makes comparisons challenging and leaves important questions relating to fitness and adaptation unanswered. For instance, it is currently difficult to disentangle the many environmental and demographic factors within and across studies potentially affecting spatial ecology in dogs to adequately compare rural and urban populations. Additionally, while it is highly likely that the different behaviours observed in different populations of free-ranging dogs constitute a component of their adaptations to human-dominated environments, 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. Furthermore, in-depth behavioural experiments have so far been limited to sites in India and Italy, though with a promising new field site in Morocco. Lastly, a substantial proportion of free-ranging dogs are likely affiliated with particular people on a more permanent basis, with some being owned, but without being restricted. Owner demographics likely have a significant impact on the behaviour of these dogs in complex interaction with ecological factors. However, the added value to our understanding of dog behaviour in a more natural setting from studying owned free-ranging individuals should not be diminished.

To move the field forward we suggest studies on free-ranging dogs at more locations, with a coordinated effort to standardize protocols and designs across global study sites for large-scale comparisons. The limited research on free-ranging dogs is particularly disappointing because the highly heterogenic environments in which dogs live on a global scale, combined with our in-depth knowledge of their evolutionary history and the advanced genetic tools specifically developed using dogs (Dutrow et al., 2022; Morrill et al., 2022; Parker et al., 2017; vonHoldt et al., 2010) offer a unique set of advantages for comparisons across populations.

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

Finally, studies on free-ranging dogs will also help advance our understanding of the behaviour of pet dogs. 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 conclusion, 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.

6. REFERENCES

Aria, M., Alterisio, A., Scandurra, A., Pinelli, C., & D'Aniello, B. (2021). The scholar's best friend: Research trends in dog cognitive and behavioral studies. *Animal Cognition*, *24*(3), 541–553. https://doi.org/10.1007/s10071-020-01448-2

Axelsson, E., Ratnakumar, A., Arendt, M.-L., Maqbool, K., Webster, M. T., Perloski, M., Liberg, O., Arnemo, J. M., Hedhammar, Å., & Lindblad-Toh, K. (2014). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, *495*(7441), 360–364. https://doi.org/10.1038/nature11837

Baan, C., Bergmüller, R., Smith, D. W., & Molnar, B. (2014). Conflict management in free-ranging wolves, Canis lupus. *Animal Behaviour*, *90*, 327–334. https://doi.org/10.1016/j.anbehav.2014.01.033

Banerjee, A., & Bhadra, A. (2022). Time-activity budget of urban-adapted free-ranging dogs. *Acta Ethologica*, *25*(1), 33–42. https://doi.org/10.1007/s10211-021-00379-6

Bensky, M. K., Gosling, S. D., & Sinn, D. L. (2013). Chapter Five - The World from a Dog's Point of View: A Review and Synthesis of Dog Cognition Research. In H. J. Brockmann, T. J. Roper, M. Naguib, J. C. Mitani, L. W. Simmons, & L. Barrett (Eds.), *Advances in the Study of Behavior* (Vol. 45, pp. 209–406). Academic Press. https://doi.org/10.1016/B978-0-12-407186-5.00005-7

Bergeron, J.-M., & Pierre, D. (1981). Le regime alimentaire du coyote (Canis latrans) et du chien errant (C. familiaris) dans le sud du Quebec. [Food habits of the coyote Canis latrans and of feral dogs C. familiaris in southern Quebec.]. *The Canadian Field-Naturalist*, *95*, 172–177.

Bergström, A., Frantz, L., Schmidt, R., Ersmark, E., Lebrasseur, O., Girdland-Flink, L., Lin, A. T., Storå, J., Sjögren, K.-G., Anthony, D., Antipina, E., Amiri, S., Bar-Oz, G., Bazaliiskii, V. I., Bulatović, J., Brown, D., Carmagnini, A., Davy, T., Fedorov, S., …

Skoglund, P. (2020). Origins and genetic legacy of prehistoric dogs. *Science*, *370*(6516), 557–564. https://doi.org/10.1126/science.aba9572

Bhattacharjee, D., & Bhadra, A. (2020). Humans Dominate the Social Interaction Networks of Urban Free-Ranging Dogs in India. *Frontiers in Psychology*, *11*:2153 https://doi.org/10.3389/fpsyg.2020.02153

Bhattacharjee, D., & Bhadra, A. (2021). Response to short-lived human overcrowding by free-ranging dogs. *Behavioral Ecology and Sociobiology*, *75*(7), 111. https://doi.org/10.1007/s00265-021-03052-x

Bhattacharjee, D., Sarkar, R., Sau, S., & Bhadra, A. (2021). Sociability of Indian free-ranging dogs (Canis lupus familiaris) varies with human movement in urban areas. *Journal of Comparative Psychology*, *135*(1), 89–97. https://doi.org/10.1037/com0000241

Bhattacharjee, D., Sau, S., & Bhadra, A. (2020). 'Bolder' together—Response to human social cues in groups of free-ranging dogs. *Behaviour*, *157*(3–4), 363–384. https://doi.org/10.1163/1568539X-bja10005

Bhattacharjee, D., Sau, S., Das, J., & Bhadra, A. (2017). Free-ranging dogs prefer petting over food in repeated interactions with unfamiliar humans. *Journal of Experimental Biology*, *220*(24), 4654–4660. https://doi.org/10.1242/jeb.166371

Boitani, L., & Ciucci, P. (1995). Comparative social ecology of feral dogs and wolves. *Ethology Ecology & Evolution*, *7*(1), 49–72. https://doi.org/10.1080/08927014.1995.9522969

Boitani, L., Ciucci, P., & Ortolani, A. (2007a). Behaviour and social ecology of free-ranging dogs. In *The behavioural biology of dogs* (pp. 147–165). CABI International.

Boitani, L., Ciucci, P., & Ortolani, A. (2007b). Behaviour and social ecology of free-ranging dogs. In *The Behavioural Biology of Dogs* (pp. 147–165). CABI Publishing, CAB Int.

Boitani, L., Francisci, F., Ciucci, P., & Andreoli, G. (1995). Population biology and ecology of feral dogs in central Italy. In *The Domestic Dog – its evolution, behaviour and interactions with people* (pp. 217–244). Cambridge University Press.

Bókony, V., Kulcsár, A., Tóth, Z., & Liker, A. (2012). Personality Traits and Behavioral Syndromes in Differently Urbanized Populations of House Sparrows (Passer domesticus). *PLoS ONE*, *7*(5), e36639. https://doi.org/10.1371/journal.pone.0036639.t007

Bonanni, R., & Cafazzo, S. (2014). The Social Organisation of a Population of Free-Ranging Dogs in a Suburban Area of Rome. In *The Social Dog* (pp. 65–104). Elsevier. https://doi.org/10.1016/B978-0-12-407818-5.00003-6

Bonanni, R., Cafazzo, S., Abis, A., Barillari, E., Valsecchi, P., & Natoli, E. (2017). Age-graded dominance hierarchies and social tolerance in packs of free-ranging dogs. *Behavioral Ecology*, *28*, 1004–1020. https://doi.org/10.1093/beheco/arx059

Bonanni, R., Cafazzo, S., Valsecchi, P., & Natoli, E. (2010). Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs. *Animal Behaviour*, *79*(5), 981–991. https://doi.org/10.1016/j.anbehav.2010.02.021

Bonanni, R., Natoli, E., Cafazzo, S., & Valsecchi, P. (2010). Free-ranging dogs assess the quantity of opponents in intergroup conflicts. *Animal Cognition*, *14*(1), 103–115. https://doi.org/10.1006/anbe.2000.1706

Bonanni, R., Valsecchi, P., & Natoli, E. (2010). Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. *Animal Behaviour, 79*(4), 957-968 http://www.sciencedirect.com/science/article/pii/S0003347210000382

Brookes, V. J., VanderWaal, K., & Ward, M. P. (2020). The social networks of free-roaming domestic dogs in island communities in the Torres Strait, Australia. *Preventive Veterinary Medicine*, *181*, 104534. https://doi.org/10.1016/j.prevetmed.2018.09.008

Butler, J. R. A., du Toit, J. T., & Bingham, J. (2004). Free-ranging domestic dogs (Canis familiaris) as predators and prey in rural Zimbabwe: Threats of competition and disease to large wild carnivores. *Biological Conservation*, *115*(3), 369–378. https://doi.org/10.1016/S0006-3207(03)00152-6

Buttner, A. P. (2016). Neurobiological underpinnings of dogs' human-like social competence: How interactions between stress response systems and oxytocin mediate dogs' social skills. *Neuroscience & Biobehavioral Reviews*, *71*, 198–214. https://doi.org/10.1016/j.neubiorev.2016.08.029

Cafazzo, S., Bonanni, R., Valsecchi, P., & Natoli, E. (2014). Social Variables Affecting Mate Preferences, Copulation and Reproductive Outcome in a Pack of Free-Ranging Dogs. *PLoS ONE*, *9*(6), e98594. https://doi.org/10.1371/journal.pone.0098594.t001

Campos, C. B., Esteves, C. F., Ferraz, K. M. P. M. B., Crawshaw Jr., P. G., & Verdade, L. M. (2007). Diet of free-ranging cats and dogs in a suburban and rural environment, south-eastern Brazil. *Journal of Zoology*, *273*(1), 14–20. https://doi.org/10.1111/j.1469-7998.2007.00291.x

Carvalho, W. D., Rosalino, L. M., Godoy, M. S. M., Giorgete, M. F., Adania, C. H., & Esbérard, C. E. L. (2019). Temporal activity of rural free-ranging dogs: Implications for the predator and prey species in the Brazilian Atlantic Forest. *NeoBiota*, *45*, 55–74. https://doi.org/10.3897/neobiota.45.30645

Chen, F. L., Zimmermann, M., Hekman, J. P., Lord, K. A., Logan, B., Russenberger, J., Leighton, E. A., & Karlsson, E. K. (2021). Advancing Genetic Selection and Behavioral

Genomics of Working Dogs Through Collaborative Science. *Frontiers in Veterinary Science*, *8:662429*. https://doi.org/10.3389/fvets.2021.662429

Cimarelli, G., Juskaite, M., Range, F., & Marshall-Pescini, S. (2023). Free-ranging dogs match a human's preference in a foraging task. *Current Zoology*, zoad046. https://doi.org/10.1093/cz/zoad046

Clancy, E. A., & Rowan, A. N. (2003). Companion Animal Demographics in the United States: A Historical Perspective. In *The state of the animals II: 2003* (pp. 9–26). Washington, DC: Humane Society Press.

Coppinger, R., & Coppinger, L. (2001). Dogs: A Startling New Understanding of Canine Origin, Behavior & Evolution. *The University of Chicago Press*.

Coppinger, R., & Coppinger, L. (2016). *What Is a Dog?* University of Chicago Press.

Coppinger, R., & Feinstein, M. (2015). *How Dogs Work*. University of Chicago Press.

Correard, S., Plassais, J., Lagoutte, L., Botherel, N., Thibaud, J.-L., Hédan, B., Richard, L., Lia, A.-S., Delague, V., Mège, C., Mathis, S., Guaguère, E., Paradis, M., Vallat, J.-M., Quignon, P., & André, C. (2019). Canine neuropathies: Powerful spontaneous models for human hereditary sensory neuropathies. *Human Genetics*, *138*(5), 455–466. https://doi.org/10.1007/s00439-019-02003-x

Cunha Silva, L., Friker, B., Warembourg, C., Kanankege, K., Wera, E., Berger-González, M., Alvarez, D., & Dürr, S. (2022). Habitat selection by free-roaming domestic dogs in rabies endemic countries in rural and urban settings. *Scientific Reports*, *12*(1), 20928. https://doi.org/10.1038/s41598-022-25038-z

Daniels, T. J., & Bekoff, M. (1989). Population and Social Biology of Free-Ranging Dogs, Canis familiaris. *Journal of Mammalogy.*, *70*(4), 754-762. http://www.jstor.org/stable/1381709

Darwin, C. (1859). *On the origin of Species*. John Murray, Albermarle Street.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. John Murray, Albermarle Street.

Duarte, J., García, F. J., & Fa, J. E. (2016). Depredatory impact of free-roaming domestic dogs on Mediterranean deer in southern Spain: Implications for human-wolf conflict. *Folia Zoologica*, *65*(2), 135–141. https://doi.org/10.25225/fozo.v65.i2.a8.2016

Duranton, C., & Gaunet, F. (2018). Behavioral synchronization and affiliation: Dogs exhibit human-like skills. *Learning & Behavior*, *46*(4), 364–373. https://doi.org/10.3758/s13420-018-0323-4

Dürr, S., Dhand, N. K., Bombara, C., Molloy, S., & Ward, M. P. (2017). What influences the home range size of free-roaming domestic dogs? *Epidemiology & Infection*, *145*(7), 1339–1350. https://doi.org/10.1017/S095026881700022X

Dutrow, E. V., Serpell, J. A., & Ostrander, E. A. (2022). Domestic dog lineages reveal genetic drivers of behavioral diversification. *Cell*, *185*(25), 4737-4755.e18. https://doi.org/10.1016/j.cell.2022.11.003

Emlen, S. T. (1982). The Evolution of Helping. I. An Ecological Constraints Model. *The American Naturalist*, *119*(1), 29–39. https://doi.org/10.1086/283888

Evans, M. J., Gibson, A., Fielding, H., Ohal, P., Pandey, P., Kumar, A., Singh, S. K., Airikkala-Otter, I., Abela-Ridder, B., Gamble, L., Handel, I., Bronsvoort, B. M. D. C., Mellanby, R. J., & Mazeri, S. (2022). Free-roaming dog population dynamics in Ranchi, India.

Research in Veterinary Science, *143*, 115–123. https://doi.org/10.1016/j.rvsc.2021.12.022

Font, E. (1987). Spacing and Social Organization: Urban Stray Dogs Revisited. *Applied Animal Behaviour Science*, *17*, 319–328.

Freedman, A. H., Gronau, I., Schweizer, R. M., Ortega-Del Vecchyo, D., Han, E., Silva, P. M., Galaverni, M., Fan, Z., Marx, P., Lorente-Galdos, B., Beale, H., Ramirez, O., Hormozdiari, F., Alkan, C., Vila, C., Squire, K., Geffen, E., Kusak, J., Boyko, A. R., … Novembre, J. (2014). Genome Sequencing Highlights the Dynamic Early History of Dogs. *PLoS Genetics*, *10*(1), e1004016. https://doi.org/10.1371/journal.pgen.1004016.s030

Gardner, H. L., Fenger, J. M., & London, C. A. (2016). Dogs as a Model for Cancer. *Annual Review of Animal Biosciences*, *4*(1), 199–222. https://doi.org/10.1146/annurev-animal-022114-110911

Gompper, M. E. (Ed.). (2014). *Free-ranging dogs and wildlife conservation* (First edition). Oxford University Press.

Gould, S. J., & Vrba, E. S. (1982). Exaptation—A Missing Term in the Science of Form. *Paleobiology*, *8*(1), 4–15. https://doi.org/10.1017/S0094837300004310

Griss, S., Riemer, S., Warembourg, C., Sousa, F. M., Wera, E., Berger-Gonzalez, M., Alvarez, D., Bulu, P. M., Hernández, A. L., Roquel, P., & Dürr, S. (2021). If they could choose: How would dogs spend their days? Activity patterns in four populations of domestic dogs. *Applied Animal Behaviour Science*, *243*, 105449. https://doi.org/10.1016/j.applanim.2021.105449

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*(1), 17–52. https://doi.org/10.1016/0022-5193(64)90039-6

Hansen Wheat, C., Fitzpatrick, J. L., Rogell, B., & Temrin, H. (2019). Behavioural correlations of the domestication syndrome are decoupled in modern dog breeds. *Nature Communications*, *10*(1), 2422. https://doi.org/10.1038/s41467-019-10426-3

Hare, B., Brown, M., Wiliamson, C., & Tomasello, M. (2002). The Domestication of Social Cognition in Dogs. *Science*, *298*(5598), 1634–1636. https://doi.org/10.1126/science.1072702

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*(9), 439–444. https://doi.org/10.1016/j.tics.2005.07.003

Hare, B., Wobber, V., & Wrangham, R. (2012). The self-domestication hypothesis: Evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, *83*(3), 573–585. https://doi.org/10.1016/j.anbehav.2011.12.007

Hare, B., & Woods, V. (2013). *The Genius of Dogs: How Dogs Are Smarter Than You Think*. Plume.

Harrington, F. H., David Mech, L., & Fritts, S. H. (1983). Pack size and wolf pup survival: Their relationship under varying ecological conditions. *Behavioral Ecology and Sociobiology*, *13*(1), 19–26. https://doi.org/10.1007/BF00295072

Hughes, J., & Macdonald, D. W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biological Conservation*, *157*, 341–351. https://doi.org/10.1016/j.biocon.2012.07.005

Hytönen, M. K., Arumilli, M., Sarkiala, E., Nieminen, P., & Lohi, H. (2019). Canine models of human amelogenesis imperfecta: Identification of novel recessive ENAM and ACP4 variants. *Human Genetics*, *138*(5), 525–533. https://doi.org/10.1007/s00439-019-01997-8

Ivanter, E. V., & Sedova, N. A. (2008). Ecological monitoring of urban groups of stray dogs: An example of the city of petrozavodsk. *Russian Journal of Ecology*, *39*(2), 105–110. https://doi.org/10.1134/S1067413608020057

Laager, M., Mbilo, C., Madaye, E. A., Naminou, A., Léchenne, M., Tschopp, A., Naïssengar, S. K., Smieszek, T., Zinsstag, J., & Chitnis, N. (2018). The importance of dog population contact network structures in rabies transmission. *PLOS Neglected Tropical Diseases*, *12*(8), e0006680. https://doi.org/10.1371/journal.pntd.0006680

Ladd, R., Meek, P., Eames, J. C., & Leung, L. K.-P. (2023). Activity range and patterns of free-roaming village dogs in a rural Cambodian village. *Wildlife Research*, *51*(1). https://doi.org/10.1071/WR23024

Larson, G., & Fuller, D. Q. (2014). The Evolution of Animal Domestication. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 115–136. https://doi.org/10.1146/annurev-ecolsys-110512-135813

Laveaux, J.-C., & King of Prussia, F. I. (1789). *The Life of Frederick the Second, King of Prussia: To which are Added Observations, Authentic Documents, and a Variety of Anecdotes*. J. Derbett.

Lea, S. E. G., & Osthaus, B. (2018). In what sense are dogs special? Canine cognition in comparative context. *Learning & Behavior*, *46*(4), 335–363. https://doi.org/10.3758/s13420-018-0349-7

Lord, K., Feinstein, M., Smith, B., & Coppinger, R. (2013). Variation in reproductive traits of members of the genus Canis with special attention to the domestic dog (Canis familiaris). *Behavioural Processes*, *92*, 131–142. https://doi.org/10.1016/j.beproc.2012.10.009

Lowry, H., Lill, A., & Wong, B. B. M. (2013). Behavioural responses of wildlife to urban environments. *Biological Reviews*, *88*(3), 537–549. https://doi.org/10.1111/brv.12012

Lubbock, J. (1884a). Teaching animals to converse. *Nature*, *29*, 216.

Lubbock, J. (1884b). Teaching animals to converse. *Nature*, *29*, 547–548.

Macdonald, D., & Carr, G. (2016). Variation in dog society: Between resource dispersion and social flux. In *The Domestic Dog: Its Evolution, Behavior and Interactions with People* (2nd edition, pp. 319–341). Cambridge University Press.

Macdonald, D. W., Campbell, L. A. D., Kamler, J. F., Marino, J., Werhahn, G., & Sillero-Zubiri, C. (2019). Monogamy: Cause, Consequence, or Corollary of Success in Wild Canids? *Frontiers in Ecology and Evolution*, *7*, 341. https://doi.org/10.3389/fevo.2019.00341

Majumder, S. S., Bhadra, A., Ghosh, A., Mitra, S., Bhattacharjee, D., Chatterjee, J., Nandi, A. K., & Bhadra, A. (2013). To be or not to be social: Foraging associations of free-ranging dogs in an urban ecosystem. *Acta Ethologica*, *17*(1), 1–8. https://doi.org/10.1644/09-MAMM-A-107.1

Makenov, M. T., & Bekova, S. K. (2016). Demography of domestic dog population and its implications for stray dog abundance: A case study of Omsk, Russia. *Urban Ecosystems*, *19*(3), 1405–1418. https://doi.org/10.1007/s11252-016-0566-9

Malcolm, J. R., & Marten, K. (1982). Natural selection and the communal rearing of pups in African wild dogs (Lycaon pictus). *Behavioral Ecology and Sociobiology*, *10*(1), 1–13. https://doi.org/10.1007/BF00296390

Mangalam, M., & Singh, M. (2013). Differential foraging strategies: Motivation, perception and implementation in urban free-ranging dogs, Canis familiaris. *Animal Behaviour*, *85*(4), 763–770. https://doi.org/10.1016/j.anbehav.2013.01.019

Marshall-Pescini, S., Schwarz, J. F. L., Kostelnik, I., Virányi, Z., & Range, F. (2017). Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. *PNAS*, *114*, 11793–11798. https://doi.org/10.1073/pnas.1709027114

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Melo, S. N. de, da Silva, E. S., Barbosa, D. S., Teixeira-Neto, R. G., Lacorte, G. A., Horta, M. A. P., Cardoso, D. T., Werneck, G. L., Struchiner, C. J., & Belo, V. S. (2020). Effects of Gender, Sterilization, and Environment on the Spatial Distribution of Free-Roaming Dogs: An Intervention Study in an Urban Setting. *Frontiers in Veterinary Science*, *7:289*. https://doi.org/10.3389/fvets.2020.00289

Miklósi, Á. (2015). *Dog Behaviour, Evolution, and Cognition* (2nd ed.). Oxford University Press.

Morrill, K., Hekman, J., Li, X., McClure, J., Logan, B., Goodman, L., Gao, M., Dong, Y., Alonso, M., Carmichael, E., Snyder-Mackler, N., Alonso, J., Noh, H. J., Johnson, J., Koltookian, M., Lieu, C., Megquier, K., Swofford, R., Turner-Maier, J., … Karlsson, E. K. (2022). Ancestry-inclusive dog genomics challenges popular breed stereotypes. *Science*, *376*(6592), eabk0639. https://doi.org/10.1126/science.abk0639

Muinde, P., Bettridge, J. M., Sousa, F. M., Dürr, S., Dohoo, I. R., Berezowski, J., Mutwiri, T., Odinga, C. O., Fèvre, E. M., & Falzon, L. C. (2021). Who let the dogs out? Exploring the spatial ecology of free-roaming domestic dogs in western Kenya. *Ecology and Evolution*, *11*(9), 4218–4231. https://doi.org/10.1002/ece3.7317

Natoli, E., Bonanni, R., Cafazzo, S., Mills, D. S., Pontier, D., & Pilot, M. (2021). Genetic inference of the mating system of free-ranging domestic dogs. *Behavioral Ecology*, *32*, 646–656. https://doi.org/10.1093/beheco/arab011

New, Jr., J. C., Kelch, W. J., Hutchison, J. M., Salman, M. D., King, M., Scarlett, J. M., & Kass, P. H. (2004). Birth and Death Rate Estimates of Cats and Dogs in U.S. Households and Related Factors. *Journal of Applied Animal Welfare Science*, *7*(4), 229–241. https://doi.org/10.1207/s15327604jaws0704_1

Ortolani, A., Vernooij, H., & Coppinger, R. (2009). Ethiopian village dogs: Behavioural responses to a stranger's approach. *Applied Animal Behaviour Science*, *119*(3–4), 210–218. https://doi.org/10.1016/j.applanim.2009.03.011

Packard, J. (2003). Wolf behavior: Reproductive, social, and intelligent. In *Wolves: Behavior, ecology and conservation.*

Pal, S. K. (2001). Population ecology of free-ranging urban dogs in West Bengal, India. *Acta Theriologica*, *46*, 69–78.

Pal, S. K. (2005). Parental care in free-ranging dogs, *Canis familiaris*. *Applied Animal Behaviour Science*, *90*(1), 31–47. https://doi.org/10.1016/j.applanim.2004.08.002

Pal, S. K. (2011). Mating System of Free-Ranging Dogs (*Canis familiaris*). *International Journal of Zoology*, *2011*, e314216. https://doi.org/10.1155/2011/314216

Pal, S. K. (2015). Factors influencing intergroup agonistic behaviour in free-ranging domestic dogs (Canis familiaris). *Acta Ethologica*, *18*(2), 209–220. https://doi.org/10.1007/s10211-014-0208-2

Pal, S. K. (2017). *Free-ranging domestic dogs in India*. LAP LAMBERT Academic Publishing.

Pal, S. K., Ghosh, B., & Roy, S. (1998a). Agonistic behaviour of free-ranging dogs (Canis familiaris) in relation to season, sex and age. *Applied Animal Behaviour Science*, *59*, 331–348.

Pal, S. K., Ghosh, B., & Roy, S. (1998b). Dispersal behaviour of free-ranging dogs Canis familiaris in relation to age, sex, season and dispersal distance. *Applied Animal Behaviour Science*, *61*, 123–132. https://doi.org/10.1016/S0168-1591(98)00185-3

Pal, S. K., Roy, S., & Ghosh, B. (2021). Pup rearing: The role of mothers and allomothers in free-ranging domestic dogs. *Applied Animal Behaviour Science*, *234*, 105181. https://doi.org/10.1016/j.applanim.2020.105181

Parker, H. G., Dreger, D. L., Rimbault, M., Davis, B. W., Mullen, A. B., Carpintero-Ramirez, G., & Ostrander, E. A. (2017). Genomic Analyses Reveal the Influence of Geographic Origin, Migration, and Hybridization on Modern Dog Breed Development. *CellReports*, *19*(4), 697–708. https://doi.org/10.1016/j.celrep.2017.03.079

Paul, M., & Bhadra, A. (2018). The great Indian joint families of free-ranging dogs. *PLOS ONE*, *13*(5), e0197328. https://doi.org/10.1371/journal.pone.0197328

Paul, M., Majumder, S. S., & Bhadra, A. (2014). Grandmotherly care: A case study in Indian free-ranging dogs. *Journal of Ethology*, *32*(2), 75–82. https://doi.org/10.1007/s10164-014-0396-2

Pavlov, I. (1927). *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex*. Oxford University Press, London.

Pérez, G. E., Conte, A., Garde, E. J., Messori, S., Vanderstichel, R., & Serpell, J. (2018). Movement and home range of owned free-roaming male dogs in Puerto Natales, Chile. *Applied Animal Behaviour Science*, *205*, 74–82. https://doi.org/10.1016/j.applanim.2018.05.022

Perri, A. (2016). A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, *68*, 1–4. https://doi.org/10.1016/j.jas.2016.02.003

Perri, A., Feuerborn, T. R., Frantz, L. A. F., Larson, G., Malhi, R. S., Meltzer, D. J., & Witt, K. E. (2021). Dog domestication and the dual dispersal of people and dogs into the Americas. *Proceedings of the National Academy of Sciences*, *118*(6), e2010083118. https://doi.org/10.1073/pnas.2010083118

Perry, L. R., Marino, J., & Sillero Zubiri, C. (2018). Going to the Dogs: Free-Ranging Domestic Dogs Threaten an Endangered Wild Canid through Competitive Interactions. *Journal of Biodiversity & Endangered Species*, *06*(01). https://doi.org/10.4172/2332-2543.1000211

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, *52*(2), 137–154. https://doi.org/10.1086/409852

Ritvo, H. (2010). *Noble Cows and Hybrid Zebras: Essays on Animals and History*. University of Virginia Press.

Russell, N. (2011). *Social Zooarcheology: Human and Animals in Prehistory*. Cambridge University Press.

Sarkar, R., Bhowmick, A., Dasgupta, D., Banerjee, R., Chakraborty, P., Nayek, A., Sreelekshmi, R., Roy, A., Sonowal, R., Mondal, B., & Bhadra, A. (2019). Eating smart: Free-ranging dogs follow an optimal foraging strategy while scavenging in groups. *Frontiers in Ecology and Evolution*, *11*, 212.

Sauvé, C. C., Berentsen, A. R., Llanos, S. F., Gilbert, A. T., & Leighton, P. A. (2023). Home range overlap between small Indian mongooses and free roaming domestic dogs in

Puerto Rico: Implications for rabies management. *Scientific Reports*, *13*(1), 22944. https://doi.org/10.1038/s41598-023-50261-7

Savolainen, P., Zhang, Y., Luo, J., Lundeberg, J., & Leitner, T. (2002). Genetic evidence for an East Asian origin of domestic dogs. *Science*, *298*(5598), 1610–1613. https://doi.org/10.1126/science.1073906

Scales, J., Hyman, J., & Hughes, M. (2011). Behavioral Syndromes Break Down in Urban Song Sparrow Populations. *Ethology*, *117*(10), 887–895. https://doi.org/10.1111/j.0030-1299.2007.15910.x

Schoener, T. W. (1971). Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*, *2*(1), 369–404. https://doi.org/10.1146/annurev.es.02.110171.002101

Schüttler, E., Saavedra-Aracena, L., & Jiménez, J. E. (2022). Spatial and temporal plasticity in free-ranging dogs in sub-Antarctic Chile. *Applied Animal Behaviour Science*, *250*, 105610. https://doi.org/10.1016/j.applanim.2022.105610

Scott, J. P., & Fuller, J. L. (1965). Genetics and the social behavior of the dog—The classic study. *University of Chicago Press*.

Scott, M. D., & Causey, K. (1973). Ecology of Feral Dogs in Alabama. *The Journal of Wildlife Management*, *37*(3), 253. https://doi.org/10.2307/3800116

Sen Majumder, S., Paul, M., Sau, S., & Bhadra, A. (2016). Denning habits of free-ranging dogs reveal preference for human proximity. *Scientific Reports*, *6*(1), Article 1. https://doi.org/10.1038/srep32014

Sih, A., Ferrari, M. C. O., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, *4*(2), 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Silva-Rodríguez, E. A., & Sieving, K. E. (2012). Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. *Biological Conservation*, *150*(1), 103–110. https://doi.org/10.1016/j.biocon.2012.03.008

Smith, D. W., Drummer, T. D., Murphy, K. M., Guernsey, D. S., & Evans, S. B. (2004). Winter Prey Selection and Estimation of Wolf Kill Rates in Yellowstone National Park, 1995-2000. *The Journal of Wildlife Management*, *68*(1), 153–166.

Switonski, M. (2014). Dog as a model in studies on human hereditary diseases and their gene therapy. *Reproductive Biology*, *14*(1), 44–50. https://doi.org/10.1016/j.repbio.2013.12.007

Tague, I. (2017). *Animal Companions: Pets and Social Change in Eighteenth-Century Britain*. Penn State University Press.

Taylor, L. H., Wallace, R. M., Balaram, D., Lindenmayer, J. M., Eckery, D. C., Mutonono-Watkiss, B., Parravani, E., & Nel, L. H. (2017). The Role of Dog Population Management in Rabies Elimination—A Review of Current Approaches and Future Opportunities. *Frontiers in Veterinary Science*, *4*, 109. https://doi.org/10.3389/fvets.2017.00109

Todes, D. P. (2014). *Ivan Pavlov: A Russian Life in Science*. Oxford University Press, USA.

Topál, J., Gergely, G., Erdõhegyi, Á., Csibra, G., & Miklósi, Á. (2009). Differential Sensitivity to Human Communication in Dogs, Wolves and Human Infants. *Science*, *325*(5945), 1269–1272. https://doi.org/10.1126/science.1176960

Vanak, A. T., & Gompper, M. E. (2010). Interference competition at the landscape level: The effect of free-ranging dogs on a native mesocarnivore. *Journal of Applied Ecology*, *47*(6), 1225–1232. https://doi.org/10.1111/j.1365-2664.2010.01870.x

Verrelli, B. C., Alberti, M., Des Roches, S., Harris, N. C., Hendry, A. P., Johnson, M. T. J., Savage, A. M., Charmantier, A., Gotanda, K. M., Govaert, L., Miles, L. S., Rivkin, L. R., Winchell, K. M., Brans, K. I., Correa, C., Diamond, S. E., Fitzhugh, B., Grimm, N. B., Hughes, S., … Ziter, C. (2022). A global horizon scan for urban evolutionary ecology. *Trends in Ecology & Evolution*, *37*(11), 1006–1019. https://doi.org/10.1016/j.tree.2022.07.012

Voltaire. (1824). *A Philosophical Dictionary: From the French*. J. and H. L. Hunt.

vonHoldt, B. M., Pollinger, J. P., Lohmueller, K. E., Han, E., Parker, H. G., Quignon, P., Degenhardt, J. D., Boyko, A. R., Earl, D. A., Auton, A., Reynolds, A., Bryc, K., Brisbin, A., Knowles, J. C., Mosher, D. S., Spady, T. C., Elkahloun, A., Geffen, E., Pilot, M., … Wayne, R. K. (2010). Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature*, *464*(7290), 898–902. https://doi.org/10.1038/nature08837

Warembourg, C., Fournié, G., Abakar, M. F., Alvarez, D., Berger-González, M., Odoch, T., Wera, E., Alobo, G., Carvallo, E. T. L., Bal, V. D., López Hernandez, A. L., Madaye, E., Maximiano Sousa, F., Naminou, A., Roquel, P., Hartnack, S., Zinsstag, J., & Dürr, S. (2021). Predictors of free-roaming domestic dogs' contact network centrality and their relevance for rabies control. *Scientific Reports*, *11*(1), Article 1. https://doi.org/10.1038/s41598-021-92308-7

Warembourg, C., Wera, E., Odoch, T., Bulu, P. M., Berger-González, M., Alvarez, D., Abakar, M. F., Maximiano Sousa, F., Cunha Silva, L., Alobo, G., Bal, V. D., López Hernandez, A. L., Madaye, E., Meo, M. S., Naminou, A., Roquel, P., Hartnack, S., & Dürr, S. (2021). Comparative Study of Free-Roaming Domestic Dog Management and Roaming

Behavior Across Four Countries: Chad, Guatemala, Indonesia, and Uganda. *Frontiers in Veterinary Science*, *8:* 617900. https://doi.org/10.3389/fvets.2021.617900

Wilson-Aggarwal, J. K., Goodwin, C. E. D., Moundai, T., Sidouin, M. K., Swan, G. J. F., Léchenne, M., & McDonald, R. A. (2021). Spatial and temporal dynamics of space use by free-ranging domestic dogs *Canis familiaris* in rural Africa. *Ecological Applications*, *31*(5), e02328. https://doi.org/10.1002/eap.2328

Wilson-Aggarwal, J. K., Ozella, L., Tizzoni, M., Cattuto, C., Swan, G. J. F., Moundai, T., Silk, M. J., Zingeser, J. A., & McDonald, R. A. (2019). High-resolution contact networks of free-ranging domestic dogs Canis familiaris and implications for transmission of infection. *PLOS Neglected Tropical Diseases*, *13*(7), e0007565. https://doi.org/10.1371/journal.pntd.0007565

Winchell, K. M., Losos, J. B., & Verrelli, B. C. (2023). Urban evolutionary ecology brings exaptation back into focus. *Trends in Ecology & Evolution*, *38*(8), 719–726. https://doi.org/10.1016/j.tree.2023.03.006

Zanin, M., Bergamaschi, C. L., Ferreira, J. R., Mendes, S. L., & Oliveira Moreira, D. (2019). Dog days are just starting: The ecology invasion of free-ranging dogs (Canis familiaris) in a protected area of the Atlantic Forest. *European Journal of Wildlife Research*, *65*(5), 65. https://doi.org/10.1007/s10344-019-1303-5

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research*, *68*, 161–190.