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Monogamy: Cause, Consequence, or Corollary of Success in Wild Canids?

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The Canidae are successful, being a widespread, abundant, speciose, and adaptable family. Several canids in particular have recently experienced rapid expansions in range and abundance, with similar situations mirrored on several continents by different species. Despite extreme behavioral diversity between and within species, monogamy is a common denominator in canid societies. In this review, we ask why canids are monogamous and how monogamy is related to their success. We begin with an overview of canid social monogamy, describing the pair bonding, paternal care, and often alloparental care that is characteristic of the family, and discuss theories on the evolution of mammalian social monogamy. We discuss why and how monogamy is maintained in canids, either voluntarily or enforced, and how ecological conditions influence either the functional advantages of monogamy or ability for enforcement and thus whether social monogamy is maintained. Social monogamy does not necessitate exclusive mating and many canids exhibit extra-pair paternity. We consider the costs and benefits of extra-pair mating for male and female canids and how ecological conditions can shift this cost/benefit balance and thus affect its prevalence. Monogamy may be responsible for many of the unusual canid reproductive characteristics through facilitating alloparental care and monogamy enforcement, and the domestic dogs' departure from monogamy supports our interpretation that it is an adaptation to resource availability. In asking whether monogamy is responsible, at least in part, for their success, we propose the *monogamy as pro-cooperative hypothesis*, suggesting four characteristics have contributed to canid success: (1) ecological flexibility, (2) high mobility, (3) high reproductive rates, and (4) sociality/cooperation, with the latter two being consequences of monogamy. These four interconnected traits enhance one another and it is their combination, with monogamy at its foundation enabling cooperative sociality and thereby enhanced reproduction and survival, that together comprise the formula of canid success.

Keywords: paternal care, alloparental care, extra-pair mating, sociality, cooperation, canidae, carnivores, pair bond

INTRODUCTION

Of their many notable attributes, three stand out about the Canidae: first, they are remarkably similar; second, they are remarkably different; and third, they are remarkably successful.

First, the similarity lies in the anatomical and behavioral traits that makes all 37 species of the family—from fennec fox (*Vulpes zerda*) to gray wolf (*Canis lupus*)—immediately recognizable as dogs (for a *dramatis personae* see Macdonald and Sillero-Zubiri, 2004). Not only are the largest species essentially morphologically inflated identikits of the smaller ones, but their expressions and demeanours are similar, as are their societies, all built around monogamy (Macdonald et al., 2004). Social monogamy is unusual amongst mammals, adopted by only 3–9% of Mammalia species and 16% of Carnivora species (Kleiman, 1977; Lukas and Clutton-Brock, 2013), yet is found in all canid species studied to date. In no other mammalian family is the pair bond so ubiquitous. In an overview of carnivore societies, Macdonald (1992) emphasized the phylogenetic descent that weaves canidness and monogamy throughout the family (as it does similarly for felidness and polygyny throughout the Felidae) (Macdonald and Kays, 2005).

Second, the canid family is highly diverse. Body sizes range from the 0.8 kg fennec fox to the 60+ kg gray wolf (Nowak, 2005). Their diets range from the almost exclusively insectivorous (e.g., bat-eared fox [*Otocyon megalotis*]) to almost exclusively carnivorous (e.g., African wild dog [*Lycaon pictus*], bush dog [*Speothos venaticus*], Ethiopian wolf [*Canis simensis*], Marino et al., 2010), with a full spectrum of omnivory between (e.g., red fox [*Vulpes vulpes*], golden jackal [*C. aureus*], African golden wolf [*C. lupaster*]). Such extremes in diets are reflected in their dentition, because while most canids have 42 teeth well-suited for generalist diets (e.g., carnassials for shearing flesh and molars for omnivory), bat-eared foxes have up to 50 less-specialized teeth (the most of any land mammal) for extreme insectivory (Klare et al., 2011), whereas the dholes, bush dogs, and African wild dogs have reduced or absent molars and enhanced carnassials for hypercarnivory (Van Valkenburgh, 1991). Canids are found in nearly all terrestrial habitats, including such extremes as Arctic tundra (Arctic fox [*Vulpes lagopus*]), desert (fennec fox), tropical forest (dhole [*Cuon alpinus*]), high-altitude environments (e.g., Ethiopian wolf, Marino, 2003; Himalayan wolf [*C.* [*lupus*] *himalayensis*], Werhahn et al., 2017, 2018) and human cities (e.g., coyote [*C. latrans*]). Some even partially exploit aquatic (e.g., short-eared dog [*Atelocynus microtis*], de Oliveira, 2009; British Columbia coastal wolf, Darimont and Paquet, 2002; Stronen et al., 2012) and arboreal (e.g., gray fox [*Urocyon cinereoargenteus*], Trapp and Hallberg, 1975) habitats. Canid social systems range from generally solitary species like the maned wolf (*Chrysocyon brachyurus*), where pairs share a territory but associate only during the mating season (Dietz, 1984), through the spatial groups of red and Arctic foxes (e.g., Hersteinsson and Macdonald, 1982, 1992), to species forming large, complex packs (e.g., Ethiopian wolves, Sillero-Zubiri and Gottelli, 1995a; bush dogs, Macdonald, 1996; African wild dogs, Creel et al., 2004; gray wolves, Jedrzejewski et al., 2005). Even within species, canids exhibit substantial variation

(Macdonald and Moehlman, 1982; Moehlman, 1989; Creel and Macdonald, 1995; Geffen et al., 1996; Moehlman and Hofer, 1997) and variability within a species may be larger than that between species (Macdonald and Moehlman, 1982; Creel and Macdonald, 1995). For example, gray wolves, coyotes, black-backed jackals (*Lupulella mesomelas*) and red foxes may live solitarily, in pairs, or in large groups (Kleiman and Brady, 1978; Messier and Barrette, 1982; Mech and Boitani, 2003; Baker and Harris, 2004; Kamler et al., 2019). Red fox home ranges vary between populations by three orders of magnitude, their societies varying between ubiquitous socially monogamous pairs and spatial groups of six adults (Macdonald, 1981), while gray wolves occupy ranges varying from 75 to 2,500 km^2 with groups varying from pairs to packs of up to 42 (Mech and Boitani, 2003). Arctic foxes can exist as a "coastal" ecotype, feeding on temporally stable seabirds and marine resources and consequently living a moderate lifestyle with litters averaging five cubs produced yearly. Alternatively, arctic foxes can exist as a "lemming" ecotype, feeding on rodents with extreme cyclic population variations and consequently mirroring this extreme lifestyle, producing litters of up to 18 cubs during rodent peaks and rarely reproducing during years of low prey availability (Tannerfeldt and Angerbjörn, 1998). Though they often exist as a single breeding pair, they may form large social groups of up to 31 individuals, referred to as "fox towns" (Elmhagen et al., 2014). Ethiopian wolves, Afroalpine specialists, also display such plasticity: pairs with large territories dominate in low productivity environments, while packs of up to 18 adults/subadults defend small territories in optimal habitats (Sillero-Zubiri et al., 2004).

Third, canids are successful, both over evolutionary and modern times. Evolutionarily, canids usurped Hyaenidae from the dog-niche in the Pliocene (Macdonald, 1992). Nowadays, many species of canids flourish alongside humanity. A canid currently claims the title of the world's most widely distributed non-domestic terrestrial mammal: the red fox (Macdonald and Sillero-Zubiri, 2004), who usurped this title from another canid, the gray wolf (Mech, 1995; Macdonald and Sillero-Zubiri, 2004), while free-ranging domestic dogs are found across the globe (Lord et al., 2013). Several canids have recently rapidly expanded their ranges: coyotes have become ubiquitous across North and Central America over the past two centuries (Gompper, 2002; Macdonald and Sillero-Zubiri, 2004), while golden jackals (Tóth et al., 2009; Rutkowski et al., 2015) and raccoon dogs (Helle and Kauhala, 1991; Kauhala and Saeki, 2004; Sutor, 2007; Kauhala and Kowalczyk, 2011) mirror this same rapid expansion across Europe. Following introductions of red foxes to Australia and eastern North America, they rapidly spread throughout most of continental Australia and USA (Kamler and Ballard, 2002). Despite intensive human efforts to control populations of red foxes, coyotes, golden jackals and free-ranging domestic dogs, these species continue to survive and thrive. Even gray wolves, driven to the brink of extinction in the 1800s, are now returning to their former range in North America and Europe (Mech, 1995, 2017; Breitenmoser, 1998; Wydeven et al., 1998; Phillips et al., 2004). That these expansions are mirrored across several parts of the world

raises the question of what has allowed these canids to achieve such wide distributions and high abundances, rapid expansion, colonization and biological invasion, and resilience to human population control.

Together, these canid attributes—similarity resulting from evolutionary conservatism and differences from behavioral flexibility—prompts the question of what are the limits to variation in each species, and if those limits differ between species, what evolutionary constraints have set them? And since the unusual common denominator of canid societies is monogamy, why are they monogamous and what role has this played in the family's success, both in evolutionary time and the Anthropocene?

Monogamy has long been an area of interest for evolutionary and behavioral ecologists (Orians, 1969; Emlen and Oring, 1977) and numerous early hypotheses attempted to explain its evolution and maintenance (e.g., Orians, 1969; Emlen and Oring, 1977; Wittenberger and Tilson, 1980). Decades of empirical and theoretical research suggest factors affecting monogamy's origin and maintenance can be complex, differ among taxa, and are subject of a constant evolutionary interplay between monogamy and associated traits (Klug, 2018; Lambert et al., 2018). However, most research on monogamy has focused on birds (Reichard and Boesch, 2003), unsurprisingly since ∼90% of bird species exhibit social monogamy. In contrast, 95–97% of studied mammals are polygamous (i.e., polygynous, polygynandrous, and less commonly, polyandrous) (Kleiman, 1977; Lukas and Clutton-Brock, 2012)—Canidae are one of the main exceptions (Kleiman, 2011). There are variations on every theme, and some cases in wild canids of polygyny, polyandry, polygynandry, plural breeding, communal breeding, cooperative breeding, and promiscuity exist. Nonetheless, we are aware of no study of any canid species that has not revealed a mated pair at its nucleus. Sexual dimorphism generally correlates with mating system (Weckerly, 1998), and amongst canids monogamous mating and paternal care are associated with little or no sexual dimorphism (Kleiman, 1977, 2011; Bekoff et al., 1981; Johnson et al., 2017). The heavy investment by females in internal fertilization, gestation and lactation leaves females committed to much of the burden of parental care and provides considerable opportunity for males to desert their partners to seek additional mating opportunities (Orians, 1969; Trivers, 1972; Maynard Smith, 1977; Clutton-Brock, 1989). Why then would canids form prolonged, year-long pair bonds, maintained not only outside of the breeding season, but often for many years? And what variations of monogamy are exhibited among and within canid species and what causes these variations?

To begin this review, we first consider social monogamy, then reveal differences between canid social and genetic mating systems, i.e., social monogamy does not dictate exclusive mating. We consider canid-specific reproductive traits that may have developed from social and genetic monogamy and, following a detour around the anomalous case of domestic dogs, we reflect on whether monogamy, and the flexible social systems built around it, is a factor in the success of members of the canid family.

CANID SOCIAL MONOGAMY

Characteristics of Canid Social Monogamy

The fundamental canid social unit, irrespective of group size, is the socially monogamous pair. The primary defining characteristic of social monogamy is spatial congruence of a single breeding male and female. However, this basic criterion is generally exceeded in canid pairs by an affiliative social pair bond, including high rates of social interaction, cooperative territorial defense, mutual offspring care, den sharing, and intrasexual aggression directed at individuals outside the pair bond (Lord et al., 2013). **Box 1** provides an overview of variations of social monogamy in canids.

Pair Bonding

Most socially monogamous animals practice serial seasonal monogamy, short-term pairing that lasts only a single breeding season, replaced by a new monogamous bond the following year (e.g., ducks of the *Anas* genus, Mock et al., 1985). Canids, in contrast, often maintain long-term affiliative and cooperative pair bonds and typically remain with the same partner, unless mortality intervenes (e.g., Island fox [*Urocyon littoralis*], Roemer et al., 2001; swift fox [*Vulpes velox*], Kitchen et al., 2005a; kit fox [*V. macrotis*], Ralls et al., 2007; cape fox [*V. chama*], Kamler and Macdonald, 2014). For example, high mortality rates were responsible for serial monogamy in populations of red foxes (Zabel, 1986), swift foxes (Kamler et al., 2004a) and in intensely hunted gray wolves (Jedrzejewski et al., 2005). Amongst Ethiopian wolves, the dominant female's position changes only with her death, though male turn-over is more frequent (Sillero-Zubiri et al., 1996a, 2004). Pairings as long as 8 years have been reported in coyotes (Hennessy, 2007) and black-backed jackals (Moehlman, 1989) and up to 9 years in gray wolves (Doug Smith, oral communication). The degree to which a pair associates outside the breeding season differs between species. For many large canids, such as gray wolves and African wild dogs, the mated pair remain closely associated year-round, coordinating their behavior and hunting together (Creel and Creel, 1995; Mech and Boitani, 2003). For small species, such as cape foxes, swift foxes, and kit foxes, mated pairs share a territory throughout the year but hunt solitarily; they share dens and closely associate only during the breeding and cub-rearing seasons whereas other times of the year they use different dens and associate with each other less frequently (Kitchen et al., 2005a; Ralls et al., 2007; Kamler and Macdonald, 2014). The maned wolf may be an extreme example of this, as mated pairs apparently do not associate with each other at all outside the of the breeding and pup-rearing season (Dietz, 1984), although intraspecific differences among populations might occur. Medium-sized canids, such as coyotes and jackals, may exhibit variations in year-around associations of mated pairs, possibly related to group size or prey size.

Paternal Care

Although paternal care occurs in only 5–10% of mammalian species (Kleiman and Malcolm, 1981; Clutton-Brock, 1991; Woodroffe and Vincent, 1994), it is nearly ubiquitous in canids (Malcolm, 1985; Asa and Valdespino, 1998; Kleiman, 2011).

BOX 1 | Variations of social monogamy in canids.

Social monogamy: Social structure involving a single breeding male and female, which in canids typically involves an affiliative pair bond, shared territory with mutual territory defense, and biparental offspring care. Group-living canids may exhibit social monogamy, with a single breeding male and female pair and additional non-breeding group members (often their offspring).

Genetic monogamy: Exclusive reproduction between one male and one female (i.e., no extra-pair paternity).

Pair bonding: Affiliative bond between a breeding male and female, which in canids is generally maintained for several years, often until the death of one of the pair. In some canids, the mated pair maintains close associations year-round, whereas in maned wolves and many small canids, although a pair shares and defends a territory year-round, close associations and den sharing occur primarily during the breeding and pup-rearing seasons (Dietz, 1984; Kitchen et al., 2005a; Ralls et al., 2007; Kamler and Macdonald, 2014).

Canid variations of social monogamy Pairs: A single pair-bonded mating male and female share a territory year-round and young disperse. Example: swift fox (Kitchen et al., 2006).

Trios: A single pair-bonded dominant mating male and female, plus an additional subordinate non-breeding adult. The additional adult is usually the offspring of at least one of the pair from a previous year, though not always. The third adult may or may not actively help in raising young, and trios may be stable over several years. Example: kit fox (White and Ralls, 1993).

Groups: A single pair-bonded dominant male and female, plus additional subordinate non-breeding adults. Additional adults are usually offspring of at least one of the pair from previous years, though not always. In some cases, additional adults may actively help in raising pups and groups may cooperatively hunt and defend resources, in which case it can be considered **cooperative breeding** (though cooperatively breeding groups could also be polygamous) Example: gray wolves (Bekoff and Wells, 1982). In other cases, additional adults do not actively help in raising pups and group members do not coordinate behavior. Example: Blanford foxes (Geffen and Macdonald, 1992).

Double litters/Plural breeding: Multiple (usually two) non-interbreeding pairs of males and females share a den and territory and produce litters. Two litters may be born in the same den (e.g., coyote: Hennessy, 2007), or two litters may later merge (e.g., arctic fox: see Norén et al., 2012). The two females are often close relatives (e.g., mother-daughter). Note that these terms have also been used to describe polygynous/polygynandrous systems. Although double litters are commonly reported in coyotes, more genetic research is needed to distinguish cases where these are in fact multiple litters or large litters with size differences between pups, or whether this represents polygamous systems, though one study has confirmed two genetically monogamous pairs (Hennessy, 2007). If alloparental care is provided to the other litter (e.g., allo-nursing between females can be common), this represents **communal breeding** (i.e., not social monogamy).

Deviations from social monogamy: Group-living canids may instead exhibit social polygyny (e.g., bigamous red foxes: Zabel and Taggart, 1989), social polyandry (e.g., African wild dogs, Spiering et al., 2010), polygynandry/communal breeding (e.g., African wild dogs, Spiering et al., 2010).

Kleiman and Malcolm (1981) categorized mammalian parental care into indirect care, which does not require physical contact with young, and direct, which does. Indirect care includes territory acquisition, maintenance and defense, shelter or den construction, anti-predator defense, and mate care through guarding and provisioning. Direct care includes huddling, grooming, transporting, feeding, active defense against predators or conspecifics and playing and socializing. In some species,

indirect paternal care predominates (e.g., Blanford's fox [*Vulpes cana*], corsac fox [*V. corsac*], Geffen and Macdonald, 1992; Asa and Valdespino, 1998; Kleiman, 2011); in others, females spend more time with the pups while males provide food (e.g., gray fox, Nicholson et al., 1985; swift fox, Poessel and Gese, 2013); in yet others, males spend more time with pups than the mother and exhibit every care-giving behavior except lactation (e.g., bat-eared fox, Malcolm, 1986; Maas, 1993; Maas and Macdonald, 2004; Wright, 2006; African wild dog, Asa and Valdespino, 1998; raccoon dog [*Nyctereutes procyonoides*], Kauhala et al., 1998). At an extreme, Kleiman (2011) reports that captive female bush dogs call their mate while giving birth, and the male helps remove pups from the birthing canal, grooms the neonates, and may help in removing the placenta (see also Macdonald, 1996).

Provisioning both the pups and lactating mother is widely documented paternal care amongst canids (Asa and Valdespino, 1998). As Macdonald (1992) noted, regurgitation of partially digested food is widely described in the lupine canid lineage (present in all species in the genera *Canis*, *Lycaon*, *Cuon*, *Chrysocyon* and *Speothos*; Biben, 1982; Johnsingh, 1982; Rasmussen and Tilson, 1984; Asa and Valdespino, 1998; Lord et al., 2013) but absent in the vulpine lineage (though see Poessel and Gese, 2013). In these more carnivorous canids, this economical means of transporting prey to the den without the risk of kleptoparasitism is clearly advantageous (e.g., van Lawick-Goodall and Lawick-Goodall, 1970). African wild dogs can carry an estimated 3 days' worth of food in their stomachs to the pups and mothers (Reich, 1981; Creel and Creel, 1995), which allows males to successfully raise pups if the mother dies (Estes and Goddard, 1967). Species feeding on medium-sized prey can carry prey to the den, allowing both parents to provision young once they are old enough to be left alone at the den (e.g., red fox, Macdonald, 1977; arctic fox, Cameron et al., 2011), but for largely insectivorous canids, this is unfeasible. In largely termitivorous bat-eared fox (Klare et al., 2011), nursing mothers must spend >85% of the night foraging (Wright, 2003), leaving males primarily responsible for guarding, huddling and grooming cubs (Lamprecht, 1979; Malcolm, 1986; Maas, 1993; Maas and Macdonald, 2004; Wright, 2006). As bat-eared fox cubs begin foraging, the male accompanies them (Wright, 2006), acting as both protector and teacher, indicating patches of food to the cubs and occasionally pre-chewing larger beetles (Maas and Macdonald, 2004). A similar division of labor is reported amongst other insectivorous canids (e.g., raccoon dog, Kauhala et al., 1998; hoary fox [*Lycalopex vetulus*], Courtenay et al., 2006), where males compensate for their inability to directly feed cubs by guarding them.

An early theory by Moehlman (1986) posited that requirements for paternal investment in canids, along with other life-history traits, relate to body size. She argued that large canids have relatively smaller infants in larger litters, requiring heavy, prolonged post-partum parental (and alloparental) investment, whereas smaller canids have relatively larger young in smaller litters, requiring less post-partum parental investment. However, other studies concluded female weight was not a strong predictor of canid litter size (Bekoff et al.,

1981; Geffen et al., 1996; but see Johnson et al., 2017) and that there was either no correlation between litter size and neonate weight (Geffen et al., 1996) or a positive correlation (Bekoff et al., 1981). Instead of body size, the need and capacity for paternal care is likely determined by diet. The greater energy requirements of large canids mean they must rely more heavily on carnivorous diets and thus larger prey, whereas smaller canids can be more omnivorous (Carbone et al., 1999; Slater, 2015). Large prey not only allow males to directly feed pups, but are also more difficult for young to learn to acquire, thus requiring a longer period of dependency and greater parental investment to ensure pups are fed; offspring even older than 1 year may be directly provisioned by adults by regurgitation in gray wolves (Mech et al., 1999) and black-baked jackals (Moehlman, 1986). With smaller omnivorous species there is less capacity and less need for males to provision young. For example, Blanford's fox males cannot economically carry insects to the cubs so they are entirely reliant on the mother's milk (Geffen and Macdonald, 1992). Diet, and more specifically prey size, therefore probably determines variations in paternal care (Kauhala et al., 1998).

Alloparental Care

Alloparental care by non-breeding adult "helpers" is widespread across canids (see Macdonald et al., 2004). Helpers are usually, but not invariably, related to the pups (e.g., Zabel, 1986; Sillero-Zubiri et al., 2004; Jedrzejewski et al., 2005). There are many examples of "helpers" benefiting pup survival. Cases of alloparenting allowing litter survival despite the mother's death have been documented in red fox (Macdonald, 1979a; von Schantz, 1984) and African wild dogs (Estes and Goddard, 1967). In black-backed jackals, the presence of one additional helper tended to result in survival of one additional pup ($R^2 = 0.89$, Moehlman, 1979). Similar but much weaker associations between pup survival and the number of helpers are found in coyotes (Bekoff and Wells, 1982) and African wild dogs (Malcolm, 1979). The presence of helpers can lead to larger litter sizes in African wild dogs (Gusset and Macdonald, 2010; Angulo et al., 2013), perhaps by increased provisioning of pregnant females. In red wolves (Canis rufus) and Ethiopian wolves, helpers increased female lifetime reproductive success by extending the female's reproductive lifespan (i.e., age of last reproduction), thereby increasing the number of reproductive events and thus lifetime reproductive success (Sillero-Zubiri et al., 2004; Sparkman et al., 2011a). Helpers reduce time pups are left unattended at the den in African wild dogs (Courchamp et al., 2002) and Ethiopian wolves (Sillero-Zubiri et al., 2004) and can actively defend against predators (Macdonald, 1979a; Bekoff and Wells, 1982; Malcolm and Marten, 1982; Creel and Creel, 1995; Kamler and Gipson, 2000; Kamler et al., 2013a).

Other studies, however, have not found helpers to be beneficial. In Blanford's foxes, non-breeding adults were not observed providing direct care to the young (Geffen and Macdonald, 1992), though perhaps they provide indirect care by territory defense or pup guarding. Helpers did not affect offspring production and/or survival in studies of Arctic foxes

(Kruchenkova et al., 2009), red foxes (Zabel and Taggart, 1989; Baker et al., 1998) and Ethiopian wolves (Sillero-Zubiri et al., 2004; Marino et al., 2012). It is, however, possible that helpers provided other benefits, such as acting as insurance if a parent dies by adopting the litter (as seen in red foxes: Macdonald, 1979a; von Schantz, 1984), or lightening the work load for the parents (as in Ethiopian wolves: Sillero-Zubiri et al., 2004), which may increase the breeding pair's future reproductive success (Marino et al., 2012, 2013). The benefit provided by helpers likely depends on ecological conditions. In gray wolves (Harrington et al., 1983) and African wild dogs (Malcolm and Marten, 1982), older siblings were observed feeding pups and thereby increasing pup survival only when there was a food availability surplus (Malcolm and Marten, 1982; Harrington et al., 1983). Furthermore, when food is scarce, not only do helpers not feed pups but will even steal food from them (Malcolm and Marten, 1982). Consequently, in lean years, pup survival can be negatively affected by competition with non-breeders (Harrington et al., 1983). Similarly, in red wolves, pup mass and survival positively correlated with the presence of helpers at low population densities, but negatively correlated with pup mass (though not survival) at high population densities. Furthermore, whilst the presence of helpers increases the breeding females' lifetime reproductive success, it can decrease the males' (Sparkman et al., 2011a). In African wild dogs, yearlings and pack size can increase pup survival (Malcolm and Marten, 1982) and there seems to be a minimum pack size threshold below which packs face an increasing probability of extinction due to the need of helpers for hunting, defense, and reproduction (i.e., an Allee effect) (Courchamp and Macdonald, 2001; Angulo et al., 2013). However, there also seems to be an optimal upper limit to pack size above which the increased competition can decrease pup survival (Macdonald and Carr, 1989; Creel and Creel, 1995). Theoretical research shows that if subordinates are related to the dominant pair, they do not need to have a positive effect to be accepted as group members and can even have a slight negative effect, if ecological constraints are such that they are unlikely to survive or reproduce if expelled from the group (Kokko et al., 2002). Dominants can increase their net fitness by allowing unhelpful or even damaging subordinates to remain in a group if it means they survive and can later reproduce (Kokko et al., 2002). Retaining subordinates in a group is often more for their benefit than that of the dominant pair (Kokko et al., 2002).

Evolution of Social Monogamy

Phylogenetic studies suggest that social monogamy has evolved independently perhaps as many as 61 times in mammals (Lukas and Clutton-Brock, 2013). Historically, suggestions for factors influencing its evolution include the need for biparental care, infanticide protection, and male mate guarding, each of which is discussed below.

Need for Biparental Care

The association between paternal care, social monogamy, and pair bonding led to an early emphasis amongst scholars on the need for biparental offspring care as the adaptive

significance of monogamy (e.g., Orians, 1969; Kleiman, 1977; Wittenberger and Tilson, 1980; Kleiman and Malcolm, 1981; Clutton-Brock, 1989). These early hypotheses suggested that if females cannot successfully rear young without help and males cannot successfully divide care between multiple litters, both would benefit from social monogamy with biparental care (Kleiman, 1977; Wittenberger and Tilson, 1980; Kleiman and Malcolm, 1981; Malcolm, 1985; Birkhead and Møller, 1996). Canids typically have a single, large litter each year (modal litter size: 3–6, Hayssen et al., 1993) and young are altricial with a long dependency period, relative to other mammals (Asa and Valdespino, 1998; Lord et al., 2013). For example, it takes as long as 8 months for pups to reach independence in black-backed jackals, side-striped jackals (*Lupulella adusta*), African golden wolves and gray wolves (reviewed in Lord et al., 2013). The commonness of canid paternal care and the prolonged post-partum parental investment required thus supported these early views that the need for male help favored the evolution of canid monogamy (e.g., Kleiman, 1977).

However, several more recent phylogenetic analyses suggest mammalian paternal care likely evolved after monogamy and that paternal care is a consequence of social monogamy, not the cause (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013; Opie et al., 2013). If both sexes are monogamous for other reasons, paternal care may be the best option to improve fitness (Emlen and Oring, 1977; Lukas and Clutton-Brock, 2013), particularly as in this situation there is high paternity assurance (Trivers, 1972; Queller, 1997; Kvarnemo, 2005; Fromhage and Jennions, 2016). Similarly, rather than large litter sizes requiring paternal care, litter size and paternal care likely coevolved (Stockley and Hobson, 2016). Canid litter sizes can be highly variable and dependent on food availability (Geffen et al., 1996; Marino et al., 2006, 2012), supported by field experiments in Arctic foxes showing provisioning increases litter sizes (Angerbjörn et al., 1991, 1995). Coevolution of paternal care and litter size resulted in larger litters which require paternal and even alloparental care to survive (Stockley and Hobson, 2016). If the need for bi-parental care was not what caused social monogamy to evolve, it is likely crucial to its maintenance (Klug, 2018).

Female choice likely contributed to the evolution of paternal care (Kvarnemo, 2005; Lukas and Clutton-Brock, 2013; Lambert et al., 2018). Kvarnemo (2005) suggested that if females select males that care for young, this can explain the correlation often observed between paternity and male care but in the opposite direction of causation to that often suggested (i.e., caring males are more likely to sire offspring, rather than males that sire offspring are more likely to provide care). This hypothesis has received far less attention than the reverse direction of causation and has been little investigated in mammals (but see Freeman-Gallant, 1996, Kvarnemo, 2005, and Alonzo, 2012 for support from invertebrates, fish, and birds). Nonetheless, there is evidence in at least one mammal: in a group-living monkey where males exhibit extreme degrees of care often toward unrelated young (Campbell, 2019), males that provide more care experience greater future mating success the following

breeding season through female choice (Ménard et al., 2001). A male would therefore directly benefit from providing care, regardless of whether he cares for his own offspring or not. Sexual selection can therefore better explain cases where males care for unrelated young (e.g., red foxes: Baker et al., 2004; bat-eared foxes: Wright et al., 2010; wolves: Cassidy et al., 2016) than natural selection (Kvarnemo, 2005; Alonzo, 2012). However, this process would only be possible where females are able to assess males' investment in young before mating and bias mating toward those males (Alonzo, 2012). While this may not apply to the majority of socially monogamous taxa that display seasonal serial monogamy, finding new partners each year (see section Pair Bonding), the long-term partnerships of canids could allow females to bias paternity based on male care provided to the previous year's litter. Male canids can vary in the quality of paternal care bestowed (e.g., bat-eared foxes, Wright, 2006), making this trait subject to sexual selection. Furthermore, even with large litters, a female can compensate for the male's work when he is absent or reduces investment (although at apparent cost to her health and survival, therefore compromising potential future reproductive success) (Sacks and Neale, 2001; Cameron et al., 2011) and females may adjust effort according to litter size (Mech et al., 1999), supporting that male care can be a female preference, rather than pure necessity. Lambert et al. (2018) suggested that monogamy and paternal care co-evolved when selection initially favored affiliative males, which subsequently evolved into paternal care.

Protection Against Male Infanticide

It had been hypothesized that infanticide may select for social monogamy in mammals. If females deter infanticide by mating promiscuously to confuse paternity, males may counter by guarding mates to ensure paternity and protect offspring (e.g., Wolff and Macdonald, 2004; Lukas and Huchard, 2014). However, phylogenetic analysis across mammals concluded that social monogamy did not evolve from high infanticide levels and that social monogamy and infanticide seemingly evolved independently (Lukas and Clutton-Brock, 2013; Lukas and Huchard, 2014).

Male Mate Guarding

Several studies concluded, based on phylogenetic and empirical evidence, that mammalian social monogamy evolved where males could not defend multiple females (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013), such as when females are solitary and occupy exclusive ranges at low density (Emlen and Oring, 1977, but also see Dobson et al., 2010). High-quality but scarce or patchy resources likely provided the selective pressures leading to social monogamy by increasing female feeding competition, resulting in female territoriality and intolerance. If breeding is also seasonal and synchronized, as with most canids (Asa and Valdespino, 1998), the temporal availability of oestrous females is also limited, such that males cannot effectively guard more than one (Lukas and Clutton-Brock, 2013). This combination of factors, making it more

beneficial for males to monopolize their current partner than seeking others, is a powerful explanation for the evolution of mammalian social monogamy (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013).

Maintenance of Social Monogamy

Social monogamy should be maintained only if (a) it is the optimal strategy for both the male and female, or (b) it is the optimal strategy for one sex and enforcement mechanisms are employed to prevent their mate from adopting other strategies, referred to as "voluntary" and "enforced" monogamy, respectively (Kvarnemo, 2018).

Voluntary Monogamy: Monogamy as the Optimal Strategy

If bi-parental care is highly beneficial or necessary for offspring survival, social monogamy may be the optimal strategy for both sexes. Because most canids are seasonal breeders (Asa and Valdespino, 1998; Lord et al., 2013), investment in one female limits the investment males can make in another (Kleiman and Malcolm, 1981). In bat-eared foxes, the best predictor of the number and proportion of surviving young is the amount of male den attendance (rather than parental age/size, territory quality, and maternal den attendance) (Wright, 2006). Males spend 30–57% of their time at the den, and a 10% increase in attendance corresponds with a 16% increase in cub survival, with complete litter survival when a male spends 49% of his time at the den (Wright, 2006; Wright et al., 2010). Males therefore cannot care for litters at two dens without severely sacrificing offspring survival at one or both. Similarly, male raccoon dogs may be required to keep pups warm while the female forages (Kauhala et al., 1998) and in black-baked jackals, an entire litter died following the male's death (Moehlman, 1986).

Enforced Monogamy: Reproductive Suppression of Subordinates

In group-living canids, social monogamy is commonly enforced by reproductive suppression of subordinates (Moehlman, 1989; Creel and Creel, 1991; Creel and Macdonald, 1995; Moehlman and Hofer, 1997; Asa and Valdespino, 1998). In a review of 25 canid species, Moehlman and Hofer (1997) found reproductive suppression in 44%. The mechanism often involves copulation interference and aggression toward same-sex individuals attempting to breed (e.g., gray wolf, Rabb et al., 1967; Derix et al., 1993; African wild dog: Malcolm, 1979; red fox: Macdonald, 1979a) and infanticide, either by directly killing subordinates' pups (African wild dog: van Lawick, 1973; dingo [*C. familiaris dingo*]: Corbett, 1988) or indirectly, such as interfering with provisioning of subordinates' pups (African wild dog: Frame et al., 1979) or causing subordinate mothers to become so excessively anxious that their offspring die from the mother's fretfulness (red fox: Macdonald, 1979a; bush dog: Macdonald, 1996).

Physiological mechanisms of reproductive suppression are less documented in canids, but there is evidence for them (e.g.,

African wild dog: Creel et al., 1997; coyote: Moehlman and Hofer, 1997; Spiering et al., 2010; Ethiopian wolf: van Kesteren et al., 2012, 2013). In Ethiopian wolves, typically only the dominant females breed during a short mating season (Sillero-Zubiri et al., 1998). A study of adjacent Ethiopian wolf packs demonstrated increased oestradiol concentration in feces from eleven dominant females but not in the nine subordinates sampled and no aggression from the dominant female preventing subordinate breeding was documented, indicating hormonal suppression of subordinate females (van Kesteren et al., 2013). Although female gray wolves can breed as yearlings (Medjo and Mech, 1976), they rarely do in the wild before age three, suggesting subordinate females may experience delayed maturation or suppressed oestrus. In African wild dogs, subordinate females were hormonally suppressed, preventing ovulation likely by elevated estrogen and estrogen/progestin ratios (Creel et al., 1997). However, the detailed physiological mechanisms involved in reproductive suppression remain unclear in many species; increased glucocorticoids from social stress is a mechanism of reproductive suppression in some other taxa (e.g., Hackländer et al., 2003), but no evidence of this has been found in canids (African wild dog: Creel et al., 1997; van Kesteren et al., 2013). Glucocorticoid levels in female African wild dogs did not differ according to dominance status (average fecal glucocorticoid concentration for dominant breeding females during the mating season was 207.47 ± 43.69 (SE) ng/g while for subordinate non-breeding females it was 202.5 ± 52.3 ng/g), suggesting other mechanisms were responsible for reproductive suppression (van Kesteren et al., 2013).

Reproductive suppression of subordinates may not be solely for the benefit of the dominant pair. Packard et al. (1983) suggest that deferred reproduction in gray wolves could have evolved by individual selection, as future reproductive fitness may be enhanced by remaining longer in a juvenile role in the native pack. Similarly, delayed dispersal in red wolf males lowers mortality, thereby increasing the chances of becoming reproductive (Sparkman et al., 2011b). Kokko and Johnstone (1999) showed that the delayed benefits of acquiring dominant status in the future ("social queuing") can provide enough incentive for subordinates to remain peacefully in a group without themselves breeding. Additionally, if larger groups experience greater survival (e.g., African wild dogs, Carbone et al., 1999), individuals may experience greater benefits by remaining as a non-breeding subordinate and helping to raise new group members, rather than dispersing to breed alone (Kokko et al., 2001). Furthermore, subordinates increase their inclusive fitness by helping to raise and improve the survival of their parents' next litter, since they are on average as closely related to their siblings as they would be to their own offspring (Moehlman, 1983, 1986).

Social dominance may play a role in reproductive suppression. Macdonald (1979a, 1987) reported that, although normally only the alpha red fox female bred, when the dominance status of the previously-alpha female waned until becoming equal with another vixen in the group, both conceived the following year. Similarly, Zabel (1986) observed that although a clear dominance relationship existed between dominant breeding females and

submissive non-related helpers, social groups with two breeding females had no obvious female dominance hierarchy.

Subordinate reproduction can also be thwarted by expelling them from the group (Jungwirth and Johnstone, 2018) or not allowing subordinates to join (e.g., females "floating" on the periphery of Ethiopian wolf groups, Sillero-Zubiri et al., 1996a; male bat-eared foxes are aggressively territorial toward young males that intrude on the territory, Maas and Macdonald, 2004). Intrasexual aggression is common in canids (e.g., Rabb et al., 1967; Kleiman and Malcolm, 1981; Zabel, 1986), as is the expulsion of same-sex subordinates. The pros and cons of tolerating additional group members are explored by Macdonald and Carr (1989). In Ethiopian wolf packs with more than one subordinate female, the mother expelled the lowest-ranking female at 18–28 months old, with assistance from the dominant sister (Sillero-Zubiri et al., 1996a). Similarly, pregnancy in subordinate Ethiopian wolves can result in pack splitting, thus restoring social monogamy (Marino et al., 2013).

Interestingly, one strategy for subordinate females to avoid reproductive suppression is to raise a litter at the edge of their parent's territory, typically with a subordinate male from a neighboring group, seen in crab-eating foxes (Macdonald and Courtenay, 1996), red foxes (Baker et al., 2000), black-backed jackals (Kamler et al., 2019) and gray wolves (Mech and Boitani, 2003). In this way, subordinates may get the best of both worlds by avoiding risky dispersal into unknown areas yet allowing reproduction. However, the tolerance of alphas letting betas raise litters and use their territory edges might vary according to food abundance and dispersion and kinship.

Ecological Correlates of Social Monogamy

Social monogamy is maintained because either it is the optimal strategy for both sexes, or because polygamy (incl. polygyny, polyandry, polygynandry) is restricted due to monogamy enforcement mechanisms or ecological conditions. Ecological conditions can shift monogamy to other social systems, either by affecting the benefits (motivations) of social monogamy itself or by affecting the ability to enforce it (summarized in **Table 1**).

Resource Availability: Paternal Care and the Polygyny Threshold Model

One of the primary benefits of social monogamy in canids is benefits to offspring survival due to biparental care (Moehlman, 1989), though resource availability affects the degree to which male care is both necessary and feasible: when resources are plentiful, females may successfully raise pups with less male input (Maas, 1993) and males are able to provide more paternal care (Wright, 2006). The polygyny threshold model (Verner, 1964, Verner and Willson, 1966, Orians, 1969) posits that there is a threshold at which a female can raise as many young sharing a male and territory of higher quality (in a polygynous system) as she could being the sole female with an inferior male/territory (in a monogamous system). Thus, if male help is required and a male cannot share care between multiple litters without decreasing the quality and offspring survival below what could be achieved with his full attention on a single litter, monogamy would be the optimal strategy. If, however, resources are such

TABLE 1 | Correlates of social and genetic monogamy in canids.

Correlate	Summary
Social monogamy vs. alternative strategies	
Resource availability	High resource availability reduces the probability of social monogamy by either reducing reliance on male care of infants and thus the benefits of monogamy or by allowing males to provision multiple litters.
Social Structure	The costs and benefits of canid group formation are influenced by many ecological factors (e.g., resource availability/dispersion, prey size, inter- and intraspecific competition, predation pressure, population density, territory availability). Larger social groups are less likely to exhibit social monogamy.
Genetic monogamy vs. extra-pair mating	
Resource availability	High resource availability reduces reliance on male care of infants and thus the potential cost of reduced male investment from engaging in extra-pair mating.
Diet: Foraging strategy	Canids that can forage with their mate can more effectively mate guard, whereas canids that must forage solitarily to reduce food competition have more opportunity to engage in extra-pair mating.
Diet: Time budget	Canids that must allocate more time to foraging (e.g., insectivorous species) have less time available to seek extra-pair mates.
Population density	High population density increases the availability of extra-pair mates and reduces potential costs of seeking extra-pair mating (reducing distances between individuals, increasing encounter rate and the probability of finding extra-pair mate).
Social structure	More potential breeders in a group increases the probability of extra-pair mating. As with population density, the costs of embarking on extra-territorial forays are reduced if extra-pair mating is within the group.

that a female can raise as many offspring in a polygynous system, either because male help is less needed or because a male can provision multiple litters as well as he could one, the "polygyny threshold" can be crossed. Supporting this, Zabel and Taggart (1989) report that when food availability was high, 71% of the island population of red foxes they studied were bigamous, i.e., a single male cared for the litters of two females, and bigamous females had equal or greater (1.4 times) reproductive success than monogamous females when considering offspring survival in the first year (mean litter size of 4.3 ± 0.29 in bigamous vs. 4.0 ± 1.0 in monogamous females, Zabel and Taggart, 1989). However, when the food supply crashed, the population shifted entirely to monogamy. Red foxes in Sweden also displayed polygyny with multiple breeding females when prey availability was high but a single breeding female when prey availability was low (von Schantz, 1984, see also West, 2014). Similarly, food availability influenced the probability of forming larger groups across four populations of arctic fox, with variations including polygyny, plural breeding and communal breeding where food abundance differed substantially between years, whereas social monogamy

is found in areas of stable resources (Angerbjörn et al., 2004; Elmhagen et al., 2014) and in marginal habitats with low food availability (Norén et al., 2012; Elmhagen et al., 2014).

Social Structure

As described in **Box 1**, canid social monogamy is not restricted to pair-living individuals but also includes group-living variations where social groups contain a single breeding male and female, in addition to non-breeding group members. Alternatively, canid groups may exhibit polygyny, polyandry, or polygynandry with multiple breeding adults. Social monogamy is, unsurprisingly, most common in smaller social groups (Clutton-Brock and Isvaran, 2006; Spiering et al., 2010). A greater availability of potential breeders is more difficult for the dominant pair to suppress (Marino et al., 2013). Spiering et al. (2010) found that many packs of African wild dogs contain only one adult female and thus inevitably only one breeding female. However, in the 30% of groups containing subordinate females, only half were socially monogamous: beta females also bred in 54.5% of years, though theta females never bred. In contrast, subordinate males always secured some paternity, but were only present in 47% of groups. Similarly, in bat-eared foxes studied by Maas and Macdonald (2004), social monogamy depended on the number of females in the group—additional females invariably bred, and in only 1 of 65 breeding events was there a non-breeding adult male in the group. In Ethiopian wolves, packs recovering from disease outbreak can become unusually large and contain more than two subordinate females, increasing the likelihood of pregnancy in subordinate females (Marino et al., 2013).

The mechanisms shaping sociality in carnivores, and in canids specifically, have been reviewed elsewhere (e.g., Macdonald, 1983; Creel and Macdonald, 1995; Macdonald and Sillero-Zubiri, 2004; Macdonald et al., 2004). Canid groups generally form by retention of offspring that do not disperse (e.g., black-backed jackal: Moehlman, 1979, 1983; red fox: Macdonald, 1980; arctic fox: Hersteinsson and Macdonald, 1982; kit fox: Ralls et al., 2001; bat-eared fox: Maas and Macdonald, 2004; hoary fox: Courtenay et al., 2006; Kamler et al., 2013b, 2019; Cape fox: Kamler and Macdonald, 2014) and thereby avoid dispersal costs (Bekoff and Wells, 1982; Macdonald and Carr, 1989; Lucas et al., 1994; Kamler et al., 2019). This results in family groups, though unrelated individuals can sometimes join existing groups (e.g., red fox: Zabel and Taggart, 1989; gray wolf: Jedrzejewski et al., 2005). Macdonald and Carr (1989), drawing heavily on canid examples, presented a profit and loss account of tolerating additional group members. A primary cost is food competition (Schmidt and Mech, 1997; Creel and Creel, 2002), but the list also includes increased risk of infectious disease (e.g., rabies, Macdonald and Bacon, 1982; Loveridge and Macdonald, 2001) and parasite transmission (Hoogland, 1979), and mate sharing (Zabel and Taggart, 1989; Spiering et al., 2010).

The adaptive functions of canid groups include greater hunting success (e.g., African wild dogs: Fanshawe and Fitzgibbon, 1993; Creel and Creel, 1995) and capacity to tackle larger prey (Fanshawe and Fitzgibbon, 1993). Larger African wild dog groups better defend food against spotted hyenas (*Crocuta crocuta*, Fanshawe and Fitzgibbon, 1993; Carbone et al., 2005),

larger golden jackal groups can steal food from smaller groups (Macdonald, 1979b) and packs of dholes can steal prey from leopards (Venkataraman and Johnsingh, 2004). Larger groups also benefit territory defense, as victory in intergroup contests generally goes to the larger group (e.g., Ethiopian wolves: Sillero-Zubiri and Macdonald, 1998; Marino et al., 2012; gray wolves: Cassidy et al., 2017). Grouping can also increase breeding success through alloparental care (e.g., Moehlman, 1979) and decreased predation vulnerability (Kamler et al., 2013a). Sociality can also provide thermoregulatory, energetic and physiological benefits through social thermoregulation (Campbell et al., 2018). Though social thermoregulation is little studied in canids, Hennemann et al. (1983) found that crab-eating foxes reduced heat loss and oxygen consumption (a measure of basal metabolic rate) by 5–18% when huddling with a partner, suggesting huddling can significantly impact daily energy expenditure in this and other canid species (Hennemann et al., 1983).

Large prey can favor cooperative hunting and larger groups (e.g., coyotes: Bowen, 1981). Intense intraspecific and interspecific competition and predation may favor group formation for strength in numbers: recolonizing gray wolves, displaying intra-guild aggression toward coyotes, led coyotes to form larger groups (Arjo and Pletscher, 1999) and higher jackal numbers increased bat-eared fox group sizes (Kamler et al., 2013a). Similarly, arctic foxes tend to form complex groups when facing greater predation pressure from red foxes (Norén et al., 2012) and a mother-daughter pair merged their litters into one den when facing red fox predation, despite low food availability at the time (B. Elmhagen, unpublished data, from Norén et al., 2012).

The costs of dispersal increase when the journey is hazardous and/or the availability of vacancies is low (Ballard et al., 1987; Norén et al., 2012). Therefore, population density, likely linked to food availability, affects the advantages of group formation such that polygamy can be associated with high population density (e.g., swift foxes, Kamler et al., 2004a; red foxes, Baker et al., 2004; Iossa et al., 2008a; gray foxes, Weston Glenn et al., 2009). Iossa et al. (2008a) found 60% of red fox groupings were socially monogamous at low population density but 23% at high population density. Similarly, in swift foxes at high population density from low predation pressure, 30% of social groups exhibited polygyny with communal denning and 40% included non-breeding females (in 10 social groups), whereas in low density/high predation pressure, only monogamy was observed, with no non-breeding helpers (16 groups, Kamler et al., 2004a).

Finally, group formation may occur not only when groups are beneficial or dispersal is costly, but rather when grouping carries little cost (Macdonald and Carr, 1989; Macdonald and Johnson, 2015). The resource dispersion hypothesis (RDH, Macdonald, 1981, 1983; Carr and Macdonald, 1986) posits that when resources are dispersed heterogeneously, the minimum territory needed to meet a breeding pair's resource requirements can often support additional group members with little or no cost to the dominant pair. Greater heterogeneity leads to larger group sizes. Macdonald (1980, 1987) reviewed the early literature to show that monogamous red fox pairs are associated with spatio-temporally homogeneous resources (e.g., farmlands

of USA Midwestern states, Storm et al., 1976), often at low population density, whereas groups more commonly form where food availability is more spatio-temporally heterogeneous and foxes that exploit cyclic rodent populations may accommodate additional group members in peak rodent years (Macdonald, 1984; von Schantz, 1984; Elmhagen et al., 2014; see also Macdonald et al., 2016). Similarly, if the cost of tolerance is low, its benefits may be minimal: Geffen and Macdonald (1992) report dominant Blanford's fox pairs tolerating non-breeding subordinate vixens, but found no evidence that they act as helpers.

The balance of these costs and benefits of group formation, determined by local ecological conditions, will therefore influence the social structure of canids and thus whether they exist as a socially monogamous pair, one of the variations on social monogamy described above, or depart from monogamy altogether.

CONTRASTING CANID SOCIAL AND GENETIC MATING SYSTEMS: POTENTIAL FUNCTIONS AND ECOLOGICAL CORRELATES OF EXTRA-PAIR MATING IN CANIDS

Social monogamy is no guarantee of genetic monogamy, i.e., exclusive mating (Klug, 2018; Lambert et al., 2018), and, indeed, almost every genetically studied canid species has revealed extra-pair paternities (EPP) (see Hennessy, 2007 for an exception). For example, extra-pair males sired 25% of 16 offspring in Island foxes (Roemer et al., 2001), 52% of 19 offspring from 15 litters in swift foxes (Kitchen et al., 2006), 31% of 176 offspring in arctic foxes (Cameron et al., 2011) and in red foxes from 38% of 38 offspring (Iossa et al., 2008b) to as much as 80% of 30 offspring (Baker et al., 2004). Many of these examples are drawn from pairs, rather than larger social groups.

In group-living canids, extra-pair mating can occur both within-pack and with extra-pack individuals. In Ethiopian wolves, despite the dominant pair's apparent social monogamy, extra-pair copulations (EPC) happen both within (rarely) and outside (more commonly) the pack (Gottelli et al., 1994): Sillero-Zubiri et al. (1996a) observed that 70% of copulations were between a female and male in adjoining packs and Randall et al. (2007) found that 50% of litters had offspring sired by an extra-pack male, with 28% of offspring with resolved paternities sired by extra-pack males. Though red wolves were found to be highly genetically monogamous, with only 4 of 174 litters (2%) showing EPP, these rare cases included extra-pair mating within and outside of the pack (Sparkman et al., 2012). In contrast, two studies in African wild dogs found that, although extra-pair mating was common, extra-pack males never sired offspring (of 226 offspring, Spiering et al., 2010, and 39 offspring, Moueix, 2006); when subordinate males existed in a pack, levels of mixed paternity in litters were 53% (of 15 litters, Spiering et al., 2010) and 100% (of 5 litters, Moueix, 2006).

Benefits and Costs of Genetic Polygyny

For males, whose reproductive success is generally limited by access to females, the benefit of extra-pair mating is obvious: mating with additional females can directly increase reproductive success by producing more offspring, and especially when these are cared for by another male. For example, male red foxes studied by Baker et al. (2004) sired more offspring with extra-pair females than with their social mate and traveled as far as 2.7 territories away during extra-territorial forays; consequently, they could have sired offspring in as many as 32 neighboring groups (Baker et al., 2004). Such males benefit doubly, genetically and from the parental investment of cuckolded males, thus extra-territorial forays are widely recorded amongst canids during the courtship and mating periods (e.g., Macdonald, 1981; Zoellick and Smith, 1992; Baker et al., 2004; Deuel et al., 2017; Kamler et al., 2017, 2019). However, the costs of male philandering include leaving their mate unguarded and therefore increasing their own risk of being cuckolded, increased exposure to sexually transmitted disease and parasites (Poiani and Wilks, 2000; McLeod and Day, 2014), and risks of mortality, predation, intraspecific conflict and stress when traveling in unfamiliar areas (Harris and Smith, 1987; Young and Monfort, 2009).

Benefits of Genetic Polyandry

For females, whose reproductive output is limited, the benefits of extra-pair mating are less obvious. Various hypotheses have been proposed to explain why females engage in extra-pair mating (summarized in **Table 2**).

Increase Genetic Quality

A favored explanation for extra-pair mating in birds is increased genetic fitness of offspring by mating with the highest quality

TABLE 2 | Potential functional explanations for extra-pair mating by female canids.

Functional hypothesis	Support in canids
Increase genetic quality	Some support. Extra-pair mating is biased toward more dominant or larger males in some canids; may depend on circumstances/species.
Increase genetic diversity	Could be a common motivation. Extra-pair mating is generally associated with multiple paternity in canids.
Inbreeding avoidance	Little support. Social pairs are generally unrelated so other mechanisms may be responsible for inbreeding avoidance, and breeding with close relatives can occur both with social mates and extra-pair mates in canids.
Infanticide protection by paternity confusion	Little support, unlikely. Infanticide does not increase males' breeding opportunities because canids breed seasonally and annually; little evidence that male canids engage in infanticide.
Fertilization assurance	Could be a common motivation due to canid monoestrum, but has not been studied.
Increased alloparental care by paternity confusion/dilution	Unlikely to apply to most cases where extra-pair mating with individuals outside the social group, but may be relevant when extra-pair mating is within the group.

males (Birkhead and Møller, 1996; Jennions and Petrie, 2000; Westneat and Stewart, 2003). In monogamous social systems where most individuals are paired, mate choice is constrained and thus most females would be partnered with suboptimal males. The majority of females would therefore benefit from seeking EPC with superior males. This may be the motivation for extra-pair mating by female red foxes studied by Iossa et al. (2008a,b). Red fox females typically engaged in EPC with dominant males from adjoining territories (Iossa et al., 2008a) and extra-pair males that sired offspring were always larger than the female's cuckolded social partner (Iossa et al., 2008b). By mating with males of higher quality than their partner, females can increase the genetic quality of their offspring. Similarly, three of four cases of EPP observed in Island foxes were by the two largest males in the study (Roemer, 1999, 2004), suggesting females engaged in extra-pair mating with high-quality males. Furthermore, multiple mating may also increase genetic quality of offspring by inciting sperm competition and allowing cryptic female choice (e.g., Kvarnemo and Simmons, 2013; Annavi et al., 2014).

Genetic quality, however, is not the only factor, as illustrated by female Ethiopian wolves that mate outside their pack being notably unselective about the dominance status of these mates (Sillero-Zubiri et al., 1996a; Randall et al., 2007) and similar observations of other red foxes being unselective outside, but selective within, the group in regards to male dominance status (Baker et al., 2004). While it is possible that females select for genetic quality using indicators other than dominance status (which is often influenced by size, health, strength), these studies suggest that, at times, other explanations are involved besides quality of the extra-pair mates (especially considering females are likely well-informed of their neighbours' social status). The case of Bristol's urban red foxes is revealing in showing how motivations for extra-pair mating can change: in 1992–1994, females appeared to be unselective in the quality of extra-group males, mating with both dominant and subordinate males (Baker et al., 2004). In 1994–1996, the population declined by 80% due to mange (Baker et al., 2000; Iossa et al., 2008a). Subsequently, in 2002–2004, females became highly selective, reducing the frequency of extra-pair mating and mating only with males that appeared to be of higher quality than their social mate (Iossa et al., 2008b). Furthermore, rates of mixed paternity dropped from 38–69% pre-outbreak to 0% post-outbreak (Baker et al., 2004; Iossa et al., 2008b). Thus, it seems that following substantial pressure from disease, females changed their reproductive strategy to emphasize genetic quality, which may increase the probability of their offspring surviving disease.

Increase Genetic Diversity

Canid litters can be sired by multiple males. Thus, polyandry might function to increase within-litter genetic diversity (Yasui, 1998; Jennions and Petrie, 2000; Slatyer et al., 2012). This was proposed to explain polyandry in arctic foxes, where 26% of litters were sired by multiple males (Cameron et al., 2011). In fluctuating environments, such as the harsh arctic, the fittest genes may be unpredictable and thus increased within-litter genetic diversity may increase the probability that at least some offspring survive (Yasui, 1998; Jennions and Petrie, 2000). The

majority of cases where female canids engage in EPC result in mixed paternity litters (e.g., Baker et al., 2004; Moueix, 2006; Randall et al., 2007; Spiering et al., 2010; Cameron et al., 2011; Converse, 2013, but see Iossa et al., 2008a,b and Cameron et al., 2011 for exceptions). Increased within-litter genetic diversity may therefore be a common motivation for extra-pair mating in canids.

Inbreeding Avoidance

Extra-pair mating may function to prevent inbreeding (Stockley et al., 1993; Jennions and Petrie, 2000; Tregenza and Wedell, 2002; Annavi et al., 2014; Arct et al., 2015). This may be particularly important where territories are inherited by successive generations or there is a lack of dispersal (e.g., Ethiopian wolf, Sillero-Zubiri et al., 1996a; bat-eared fox, Maas and Macdonald, 2004), leading to highly related groups. However, in most canids that have been genetically investigated, mated pairs are generally unrelated (e.g., African wild dog: McNutt, 1996; Girman et al., 1997 [average relatedness of social pairs: 0.05 ± 0.11, $N = 5$]; gray wolf: Smith et al., 1997 [0.01 ± 0.14, $N = 16$]; arctic fox: Cameron et al., 2011 [0.01 ± 0.14, $N = 13$]; kit fox: Ralls et al., 2001 [-0.07 ± 0.07, $N = 10$]; coyote: Hennessy, 2007 [0.00 ± 0.14, $N = 7$]; swift fox: Kitchen et al., 2006 [-0.01 ± 0.23, $N = 48$]; red wolf: Sparkman et al., 2012, $R < 0.50$ for 95% of 174 mating events). Although there are occasional instances where social pairs are closely related (e.g., Hennessy, 2007: 1/7 coyote pairs, $R = 0.26$; Kitchen et al., 2006: 1/48 swift fox pairs, $R = 0.48$; Weston Glenn et al., 2009: one gray fox pair, $R = 0.36$; Roemer, 1999: 4/15 Island fox pairs, $R = 0.19, 0.35, 0.35, 0.52$; Jedrzejewski et al., 2005: one gray wolf half-sibling pair), there are also cases where extra-pair mating occurs between relatives. For example, Baker et al. (2004) found four incestuous EPPs between close relatives with experiential histories (mother-son for 2 years, father-daughter, and half-brother-half-sister) and three additional pairings between more distantly related individuals (e.g., $R = 0.13$) in red foxes, Cameron et al. (2011) found one incestuous mother-son case of EPP (of 13 mated pairs, 7.6%) between arctic foxes that were socially paired with non-relatives, and Sparkman et al. (2012) found 4 parent-offspring and 4 full-sibling matings (of 174 mated pairs, 9%). There may be greater risk of this where there is neighborhood settlement by dispersers, as in crab-eating foxes (Macdonald and Courtenay, 1996), bat-eared foxes (Kamler et al., 2013b), swift foxes (Kitchen et al., 2005b) and black-backed jackals (Kamler et al., 2019). When it has been investigated, relatedness between social mates and extra-pair mates did not differ (e.g., Cameron et al., 2011: mean $\pm$ SD relatedness between social mates: 0.05 ± 0.12, $N = 9$; between extra-pair mates: -0.09 ± 0.11, $N = 4$). It therefore seems that canids achieve inbreeding avoidance by other mechanisms, such as avoiding mating within ones' natal pack, sex-biased dispersal and adult dispersal (Kamler et al., 2004c, 2013b; Geffen et al., 2011; Sparkman et al., 2012; Kamler and Macdonald, 2014).

One exception, however, could be in Ethiopian wolves. A lack of dispersal opportunities from shrinking habitat, coupled with male philopatry, results in highly related packs (Sillero-Zubiri et al., 1996a; Randall et al., 2007). Sillero-Zubiri et al. (1996a)

observed that the majority (70%) of copulations by female Ethiopian wolves were with males from adjoining packs, rather than her own pack, and thus extra-pack mating was suggested to be an inbreeding avoidance strategy. Females rejected advances from all males within their packs except those from the alpha male, yet were unselective concerning the status of extra-pack males with which they mated, suggesting outbreeding was of importance rather than mate quality (Sillero-Zubiri et al., 1996a). However, subsequent research found that, although packs are indeed highly related (mean pairwise relatedness within packs was 0.39) and there is a high prevalence of incestuous pairing (22% of mating pairs within packs were closely related [$R = 0.18$–0.44]), members of neighboring packs were also closely related so incestuous pairing occurred with both within-pack and extra-pack mating (33% of extra-pack mating pairs were closely related [$R = 0.42$–0.44]). In this case, female dispersal appears to contribute more than extra-pack mating to reduce inbreeding (Randall et al., 2007). Was this an artifact of the unusual, modern, circumstances of these wolves? Perhaps extra-pack mating evolved as an inbreeding avoidance strategy, but modern conditions, exacerbated by recurrent rabies outbreaks (Mebatsion et al., 1992; Sillero-Zubiri et al., 1996b; Whitby et al., 1997; Randall et al., 2004, 2006; Marino et al., 2006), changes in dispersal and demographic events led to neighboring packs and breeding pairs being more closely related than during evolutionary time (Randall et al., 2007).

Infanticide Protection by Paternity Confusion

Based on evidence across 33 mammal families, Wolff and Macdonald (2004) concluded that the most convincing explanation for polyandry across mammals is paternity confusion to deter infanticide. This hypothesis, originally proposed by Hrdy (1974, 1979), relies on female promiscuity being an effective counterstrategy against male infanticide (Lukas and Huchard, 2014) and predicts that females mate with many males. However, a complication is that, in contrast to some taxa (notably felids, see Macdonald et al., 2010), male infanticide in canids would not hasten female oestrus because most canids are seasonal breeders (Asa and Valdespino, 1998; Valdespino et al., 2002; Lord et al., 2013), notwithstanding some possible exceptions in African wild dogs (Frame et al., 1979), bat-eared foxes (Rosenberg, 1971), and bush dogs (Porton et al., 1987). This raises the question of what male canids could gain by infanticide. Indeed, amongst canids infanticide appears most commonly practiced by females (e.g., African wild dog: van Lawick, 1973; coyote: Camenzind, 1978; dingo: Corbett, 1988; gray wolf: McLeod, 1990; Ethiopian wolf: Sillero-Zubiri et al., 1996a; Girman et al., 1997), either as suppression of subordinate breeding attempts by the dominant female (Corbett, 1988; McLeod, 1990; Sillero-Zubiri et al., 1996a; Girman et al., 1997) or perhaps to increase availability of breeding territories or dens (see Zabel, 1986). Although examples of male infanticide are numerous amongst ursids and felids (e.g., Loveridge et al., 2007), we know of none in canids. The closest reports seem to be a description of a lone female red fox being harassed by males who intruded on her den and eventually the entire litter died (Zabel, 1986; Zabel and Taggart, 1989) and Latham and Boutin

(2011) suggested that the death of a gray wolf pup may have been infanticide by a male, though the evidence was inconclusive and might best be explained by intergroup resource competition. Furthermore, in contrast to infanticidal male takeovers in other taxa (e.g., Loveridge et al., 2007), quite the opposite has been reported in gray wolves: when a new and unrelated alpha wolf takes over a pre-existing pack, he provisions and cares for pups that are not his own, which may increase his acceptance by the pack (Cassidy et al., 2016). Thus, paternity confusion to prevent infanticide is an unconvincing explanation for extra-pair mating in canids.

Fertilization Assurance

Females may engage in EPC for fertilization assurance to guard against male infertility (Wetton and Parkin, 1991; Hoogland, 1998; Hasson and Stone, 2009). Canids are unusual among Carnivora in that they are monoestrous, having only one ovulation event each season (Asa and Valdespino, 1998; see section Monoestrum), making the stakes high if a female's mate is infertile. Multiple mating may guard against this possibility.

Alloparental Care From Paternity Confusion/Dilution

In communal or cooperative breeding situations, selective female promiscuity with group members could be beneficial by confusing or diluting paternity and thus potentially increasing offspring care, particularly when paternal care is indivisible. This would not apply to most cases of EPC in canids where mating occurs outside of the social group (e.g., Sillero-Zubiri et al., 1996a; Baker et al., 2004). However, in African wild dogs, despite previous beliefs that only the alpha pair breeds, research found females frequently mate with subordinate males and documented high levels of paternity sharing, though none of the offspring analyzed (39 pups, Moueix, 2006; 226 pups, Spiering et al., 2010) were sired by extra-pack males. Spiering et al. (2010) found that the three top-ranking males always sired pups, or, if there were only two males in a pack, they shared the litter's paternity equally (similarly see Moueix, 2006). Male African wild dogs invest heavily in offspring care (Creel et al., 2004) so by mating with multiple males in a group, females may dilute paternity and increase the amount of care for her offspring while also increasing within-litter genetic diversity.

Costs of Genetic Polyandry

Like males, females engaging in extra-pair mating risk increased exposure to sexually transmitted disease and parasites (Poiani and Wilks, 2000; McLeod and Day, 2014) and increased stress (Young and Monfort, 2009) and mortality (Harris and Smith, 1987). Additionally, females may lose investment in her offspring by her mate or other group members.

Loss of Paternal Care

If males adjust investment according to confidence in paternity (Trivers, 1972; Møller and Birkhead, 1993; Sheldon, 2002), females should be less likely to seek EPCs when paternal care is important (Mulder et al., 1994; Westneat and Stewart, 2003; Lambert et al., 2018). Such reduced paternal investment by males with unfaithful partners is observed in arctic foxes: Cameron et al.

(2011) found that, in faithful partnerships, den attendance rates were similar for males and females, whereas cuckolded males showed a 56% reduction in den attendance compared to non-cuckolded males and a non-significant 52% reduction in food provisioning. Overall rates of food provisioning did not differ between litters, meaning greater burden of care was placed on unfaithful females. The potential costs to males were substantial: 11% of litters were cared for by a male that did not sire any of the offspring. In contrast, in bat-eared foxes, cuckolded males did not invest less than other males (Wright et al., 2010). One explanation for this difference is that, because canids can have mixed paternity litters, when male care is indivisible among pups, such as vigilance against predators, females may be able to get away with some EPP without reducing male investment. Amongst bat-eared foxes, male den attendance is important and cannot be split amongst the young, whether sired by that male or not; conversely, food provisioning by male arctic foxes could be preferentially directed toward their own progeny, although this is untested (Wright et al., 2010; Cameron et al., 2011). However, this presupposes males can recognize their own offspring, which may be unlikely considering success of cross-fostering in coyotes (Kitchen and Knowlton, 2006), red wolves (Gese et al., 2015), gray wolves (Goodman, 1990; US Fish Wildlife Service, 2004) and dingoes and African wild dogs (Kitchen and Knowlton, 2006) and cases where cuckolded male foxes care for litters sired entirely by other males (Baker et al., 2004; Cameron et al., 2011). An alternative explanation for this difference between arctic and bat-eared foxes relates to the potential risk and costs. Comparative research across taxa suggests males reduce investment when cuckolded only when there is high cost and high risk of cuckoldry (Griffin et al., 2013). EPP was twice as frequent in arctic foxes as in bat-eared foxes and arctic males faced high potential costs of caring for litters sired entirely by other males (Wright et al., 2010; Cameron et al., 2011). A third explanation relates to female choice: if females preferentially mate with males that provide care, males can increase future breeding success by caring even for unrelated young (Kvarnemo, 2005; Alonzo, 2012; see section Need for Biparental Care). If females adjust the amount of extra-pair mating according to levels of male care (as in some birds: Freeman-Gallant, 1996), this can even paradoxically result in greater male investment when cuckolded to avoid losing future breeding opportunities.

Loss of Alloparental Care
A similar potential cost to engaging in extra-pair mating is the possible loss of alloparental care by philopatric young (who might otherwise be assumed to be related to new pups as full sibs). However, although there is little research on how EPP affects alloparental care, increased inclusive fitness is not the only motivation for alloparenting. Helpers are not always related to pups (Zabel, 1986) and may receive other benefits, such as inheritance of dens/territories (Lindström, 1986; Zabel, 1986; Kokko et al., 2002; Marino et al., 2012, 2013; Converse, 2013) or dominance status (Baker et al., 1998; Kokko and Johnstone, 1999), or where individuals achieve greater fitness by being in larger groups (e.g., African wild dogs: Carbone et al., 1999), thus making alloparental care beneficial even when

helpers are unrelated to the young ("group augmentation"; Kokko et al., 2001).

Ecological Correlates of Extra-Pair Mating
Ecological conditions can affect the balance of these costs and benefits of extra-pair mating and thus its prevalence (summarized in **Table 1**).

Resource Availability and Reliance on Paternal Care
When resources are abundant, offspring survival may be less dependent on male care and thus the potential costs of EPCs may be outweighed by potential benefits (Norén et al., 2012). Though desirable, there are cases where paternal care is not essential and females can at least sometimes raise litters without male assistance (e.g., bat-eared fox: Maas, 1993; coyote: Sacks and Neale, 2001; swift fox: Kamler et al., 2004b; cape fox: Kamler and Macdonald, 2014). This leads to the prediction that in socially monogamous species with biparental care, EPCs should increase with increased resource availability; a prediction supported for birds (Møller, 2000; Griffith et al., 2002). A comparative analysis of 15 mammal species (including three canids) found that rates of EPP correlated with levels of paternal care (Huck et al., 2014; see also Dillard and Westneat, 2016). Similarly, EPCs may be more common in mammals than in birds because paternal care is more common in birds (Isvaran and Clutton-Brock, 2006).

Within canids, among the lowest reported values of EPP thus far found is in bat-eared foxes (9.8–15.6%, Wright et al., 2010), a species wherein male care can be highly beneficial for offspring survival (Wright, 2006). The frequency of EPP in arctic foxes studied by Cameron et al. (2011) was argued to reflect variations in the need for paternal care: EPP correlated with spatial variation in food availability, being more frequent when closer to a goose colony. However, this study did not control for effects of population density, which often correlates with resource availability (e.g., Clark, 1972; White and Garrott, 1997) and thus could have been responsible for greater EPP closer to the goose colony. However, this hypothesis was not supported in a study of urban coyotes, wherein despite optimal food availability, pairs were strictly genetically monogamous (96 offspring from 18 litters, Hennessy et al., 2012).

Diet (Foraging Strategy and Time Budget)
Mate guarding is a common strategy to prevent EPCs, though the feasibility is affected by mate proximity during foraging and/or foraging time budgets. Solitary foragers (e.g., Island fox: Roemer, 1999; red fox: Baker et al., 2004; swift fox: Kitchen et al., 2006; Iossa et al., 2008a; Arctic fox: Cameron et al., 2011) may have greater opportunity to engage in clandestine EPCs, allowing relatively high levels of EPP (Island foxes: 25%, Roemer, 1999; red fox: 38–80%, Baker et al., 2004; Iossa et al., 2008b; swift fox: 52%, Kitchen et al., 2006; Arctic foxes: 31%, Cameron et al., 2011). These typically solitary foragers apparently try to reduce EPCs by spending more time closer to their partners during the breeding season (Kitchen et al., 2005a). In contrast, the relatively low levels of EPP in bat-eared foxes (9.8–15.6%, Wright et al., 2010) may reflect their insectivorous diet which enables partners to forage together (Wright, 2003). Additionally, insectivorous

species with high foraging requirements may not have time to search for extra-pair mates: bat-eared foxes spend 80% of the night feeding (Wright et al., 2010), leaving little free time to search for extra-pair mates.

Population Density

Population density and female dispersion can be key factors affecting levels of EPC (Iossa et al., 2008a). High population density decreases the potential risks of embarking on extra-territorial forays to search for mating opportunities by decreasing distances between individuals, increasing encounter rates between males and females seeking EPCs and allowing males to assess the reproductive conditions of neighboring females (Gorman and Trowbridge, 1989). High population densities are associated with high levels of EPP in red foxes (up to 80% of cubs sired by extra-pair males at a density of 19.6–27.6 adults/km^2; Baker et al., 2004) and Island foxes (25% of 16 offspring sired by extra-group males with population density of 2.4–15.9 foxes/km^2; Roemer et al., 2001).

Particularly compelling evidence of the effect of population density on extra-pair mating comes from a population of red fox that experienced severe population declines while food availability remained constant. In a shift from high density (19.6–27.6 adults/km^2) to low (4.0–5.5 adults/km^2) from mange outbreak, EPP rates decreased from 80% (30 offspring) to 38% (38 offspring) and multiple paternity rates of litters decreased from 38–69% (16 litters) to 0% (10 litters, Baker et al., 2004; Iossa et al., 2008a). Fox body mass did not differ between the high and low density periods, indicating the population was not resource-limited at high densities (Soulsbury et al., 2008), suggesting food availability was not responsible for these differences.

However, population density did not seem to affect EPP in swift foxes studied by Kitchen et al. (2006) and urban coyotes living at high density with high resource availability were entirely genetically monogamous (Hennessy et al., 2012).

Social Structure

The number of potential breeders in a group influences the probability of extra-pair mating in canids (Spiering et al., 2010) and in mammals more generally (Clutton-Brock and Isvaran, 2006; Isvaran and Clutton-Brock, 2006; Lambert et al., 2018). Thus, the factors affecting group formation (described in section Ecological Correlates of Social Monogamy: Social Structure) can influence EPC.

THE UNUSUAL CANID REPRODUCTIVE SYSTEM: ANOMALOUS CANID REPRODUCTIVE TRAITS AND THEIR POTENTIAL RELATIONSHIP WITH MONOGAMY

Canids exhibit a suite of reproductive and physiological features that are unusual or even unique among mammals (Asa and Valdespino, 1998). The ultimate cause of these unusual traits could relate to the monogamous social system of canids by facilitating alloparental care and enforcing monogamy.

Facilitation of Alloparental Care

Long-term monogamous mating results in high levels of kinship between group members, an important factor in the evolution of mammalian alloparental care and cooperative breeding (Lukas and Clutton-Brock, 2012). Phylogenetic research shows that mammalian cooperative breeding evolved from social monogamy (Lukas and Clutton-Brock, 2012; Dillard and Westneat, 2016). Canids have developed several physiological characteristics that facilitates caring of offspring by individuals other than the mother, including the ability to provide food through regurgitation, obligate pseudopregnancy with potential spontaneous lactation, and seasonal prolactin surges. The conflict between whether to help raise siblings or breed is minimized since older offspring of a monogamous pair are equally related to their full-siblings as they would be to their own offspring.

Regurgitation

An innovation in canids is the ability to directly feed both pups and mother by regurgitation of partially digested food. This ability is found in all wolf-like canids (*Canis, Cuon,* and *Lycaon* genera, Johnsingh, 1982; Lord et al., 2013) as well as maned wolves (Rasmussen and Tilson, 1984) and bush dogs (Biben, 1982). Regurgitation is generally absent from vulpine canids, although it was recently reported in the swift fox (Poessel and Gese, 2013). Regurgitation may be seen as an evolutionary adaptation facilitating paternal care, alloparental care and cooperative breeding, which would be advantageous in a closely-related monogamous social system.

Hormonal Priming of Alloparental Care

Canid ovulation that does not result in pregnancy is followed by a remarkably long dioestrous phase of nearly the same duration as pregnancy (2 months, Asa and Valdespino, 1998), during which time progesterone and prolactin are elevated, similar to pregnancy. This is therefore called pseudopregnancy. Spontaneous ovulation followed by obligate pseudopregnancy with hormonally-primed allomaternal care and the potential for additional lactating females has clear benefits for helping the pack and caring for the dominants' offspring.

All canid species whose reproductive physiology have thus far been studied exhibit obligate pseudopregnancy, including gray wolves, coyotes, arctic foxes, red foxes, Ethiopian wolves and culpeos (*Lycalopex culpaeus,* Asa, 1997; Asa and Valdespino, 1998; van Kesteren et al., 2013). The endocrine similarity of obligate pseudopregnancy to true pregnancy hormonally primes all females that have ovulated for maternal behavior, regardless of whether they conceived, thereby encouraging allomaternal care by non-breeding subordinate females. The hormonal similarity of pseudopregnancy and pregnancy can even cause spontaneous lactation, providing the possibility for females aside from the mother to nurse pups (Jöchle, 1997; Asa and Valdespino, 1998; van Kesteren et al., 2013). Allonursing has been reported in all *Canis* species except golden jackals (Lord et al., 2013) and can increase pup survival (Sillero-Zubiri et al., 2004). The potential for allo-suckling may be an adaptive function of pseudopregnancy (Macdonald, 1992; Jöchle, 1997). In gray wolves, all pack members experience seasonal peaks in prolactin

coinciding with pup birth. All adult wolves, even gonadectomized individuals, experience this prolactin peak, which is identical for males and females (Kreeger et al., 1991). Prolactin is associated with parental care in other species (reviewed by Angelier and Chastel, 2009) and thus this is likely related to the parental care exhibited by all pack members, including males (Kreeger et al., 1991; Jöchle, 1997).

Monogamy Enforcement
Post-copulatory Lock
A post-copulatory tie has been reported for all canid species where copulation was observed, though of varying duration (Asa and Valdespino, 1998). In African wild dogs, the lock can be very brief (Asa and Valdespino, 1998), while in fennec foxes, locks can last as long as 2.75 h (average 1.8 h, Valdespino et al., 2002). The function may be to increase the probability of fertilization and enhance sperm transport. It has also been suggested to be an anatomical adaptation to encourage monogamy as a form of post-copulatory mate-guarding, since no other males can access the female during the period of sperm transport (Gomendio, 1998).

Monoestrum
The only carnivores to exhibit monoestrum, the restriction of seasonal reproduction to a single ovulatory cycle (Asa and Valdespino, 1998), are canids and their close relatives, ursids (Hayssen et al., 1993; Agnarsson et al., 2010). Polyoestrum, which is typical of most other mammals, is characterized by successive cycles of oestrus and ovulation without an intervening period of anoestrus (reproductive quiescence), which can be seasonal or year-round. Thus, if a female fails to conceive at one ovulation she has additional opportunities. Seasonal monoestrum limits females to a single conception opportunity per year—potentially a very risky reproductive strategy.

In ursids, the risk of monoestrous leading to missed mating opportunities is reduced by induced ovulation, meaning females only ovulate in the presence of appropriate stimuli (e.g., a male or copulation), similar to many other Carnivora species (e.g., felids, mustelids, Hayssen et al., 1993). Canids, however, not only have a single ovulatory cycle per season, but also exhibit spontaneous ovulation (Conaway, 1971; Asa and Valdespino, 1998), seemingly a derived trait as there is evidence of induced oestrus and ovulation in the most basal canid genus, *Urocyon* (Lindblad-Toh et al., 2005): Island foxes (*U. littoralis*) ovulate only in the presence of males (Asa et al., 2007) (whether there is induced oestrus and ovulation in the other member of the *Urocyon* genus [e.g., gray fox, *U. cinereoargenteus*] is unknown). Canids are thus unique in that they exhibit both spontaneous ovulation and monoestrum. This combination may increase the value of long-term pair bonding. Although the risks of monoestrous are reduced by the long oestrous period in canids (lasting ∼1 week, contrasting with the 1-day oestrous of many mammals, Asa and Valdespino, 1998), with only a single spontaneous oestrous cycle per year, there would be considerable risk if a female does not find a partner during the limited window of reproductive opportunity or if a female unknowingly paired with an infertile or genetically

incompatible mate; long-term successful pairing may provide assurance against these possibilities.

Asa and Valdespino (1998) argue that the ultimate cause for monoestrum could be the canid social system, facilitating social monogamy and cooperative breeding through reproductive suppression. Monoestrum eliminates the opportunity for additional periods of oestrus in subordinates, which could cause social tension. They argue that if canids were polyoestrous, the dominant female would likely conceive on the first cycle but subordinates would continue cycling. However, due to canids' long oestrous period (Asa and Valdespino, 1998), the duration of time in oestrus may be equivalent between monoestrum and polyoestrum, resulting in the same amount of effort needed for reproductive suppression, regardless if over several cycles or one.

THE EXCEPTION PROVES THE RULE: SOCIAL AND MATING SYSTEM OF THE DOMESTIC DOG

The domestic dog presents an interesting case because its social and mating system differs from all other members of the *Canis* genus. Domestic dogs derived from the gray wolf an estimated 11,000–40,000 years ago (see reviews by Driscoll et al., 2009; Driscoll and Macdonald, 2010; Wang et al., 2013; Frantz et al., 2016; Botigué et al., 2017). Despite their close evolutionary history, the general *Canis* pattern of social monogamy, pair bonding, extended paternal and alloparental care and monoestrous seasonal reproduction is conspicuously absent from dogs (Lord et al., 2013).

Free-living dogs generally exhibit a promiscuous mating system with no breeding hierarchy (Lord et al., 2013), though they can exhibit a range of mating systems (Pal, 2011). All adults can have the opportunity to breed and thus dog social groups can contain multiple lactating females with litters, in addition to other male and female group members (Macdonald and Carr, 1995; Pal, 2011; Paul et al., 2014). Though free-living dogs often live in groups, they do not always form a structured pack (Macdonald and Carr, 1995; Kamler et al., 2003a; Majumder et al., 2014). A social group may defend a territory together, but groups can be dynamic in composition, influenced by mating interests, resource availability, and closeness to source populations (Macdonald and Carr, 1995; Kamler et al., 2003a; Majumder et al., 2014). Some groups hunt cooperatively (Kamler et al., 2003b; Fleming et al., 2006) while others seemingly do not (Macdonald and Carr, 1995). Care is predominantly provided by the mother (Macdonald and Carr, 1995; Lord et al., 2013), though there are some observations of paternal (Pal, 2005) and alloparental (Paul et al., 2014) care. Although regurgitation and provisioning of offspring by males and helpers is characteristic of all other *Canis* species, it is rare in domestic dogs and mainly exhibited by the mother (Malm, 1995; though see Pal, 2005; Lord et al., 2013). Dogs reach independence much earlier than other *Canis* species, at 10–13 weeks, compared to an approximate average age of 6 months for other members of the genus (Pal, 2005; Lord et al., 2013). Dog pups do not receive extended parental care. After weaning, dog pups are independent of

parenting and no longer directly fed; they instead must find their own food and compete with adults and juveniles. Wild *Canis* all exhibit reproductive seasonality, including dingoes, with births coinciding with seasonal increases in food availability; dogs are the only exception, with females coming into oestrous approximately every 7 months and males always being capable of reproducing, though there can be concentrations of breeding during certain times of the year (Lord et al., 2013). Thus, dogs exhibit approximately two oestrus per year, unlike all other monoestrous *Canis* (Asa and Valdespino, 1998; Lord et al., 2013). This vastly different social and mating behavior of domestic dogs compared to wild *Canis* is associated with different ecological conditions, providing an opportunity for understanding the ecological conditions that shape monogamy in other canids.

Are These Differences Adaptive?

Although Macdonald and Carr (1995) cautioned against interpreting the behavior of a domesticated species as adaptive, Lord et al. (2013) argue that humans have had little reproductive control over the vast majority of dogs because most are free-ranging. They argue that the differences in the reproductive systems and behavior of dogs compared to other *Canis* are adaptations to a new ecological niche created by the permanent and stationary settlement of humans and the associated food resource availability, rather than by artificial selection or reduced natural selection. The proposition that their behavior is adaptive is supported by findings that two different dog communities behaved very differently when exposed to contrasting ecological circumstances (Macdonald and Carr, 1995).

Dogs tend to cluster in areas of human waste and the diet of most free-ranging dogs originates from humans, either directly through provisioning or indirectly from scavenging (Kamler et al., 2003a; Vanak and Gompper, 2009). Dogs are therefore released from seasonal fluctuations in resource availability, avoid high costs of having to hunt and generally experience high resource abundance (Macdonald and Carr, 1995; Kamler et al., 2003a; Pal, 2008; Lord et al., 2013). The ease of finding and processing food decreases the necessity for energetically-expensive parental care behaviors, making male care less valuable for domestic dogs than for wild canids. The reliable, year-round availability of human-derived food likely favored the loss of reproductive seasonality (Lord et al., 2013). Freed from seasonality in resource availability, dogs can breed continuously throughout the year, avoiding competition with other dog litters even within the same social group. This also allows early age at first reproduction as dogs can breed as soon as they come into maturity, rather than waiting for the next breeding season (Lord et al., 2013). By avoiding energetically-costly parenting behavior, dog parents can redirect energy into breeding year-round and multiple times per year, thereby increasing fecundity (Lord et al., 2013).

Although for wild canids the optimal strategy for maximizing reproductive success is often monogamy with biparental care, for domestic dogs paternal and alloparental care is not necessary due to more stable resource availabilities and thus they benefit from adopting an entirely different strategy. The genus-atypical reproductive and parental behavior of domestic dogs supports the hypothesis that monogamy in canids is largely an adaptation allowing wild canids to make the most of fluctuations in resource availability (Lord et al., 2013).

CANID SUCCESS: CAUSE, COROLLARY OR CONSEQUENCE OF MONOGAMY, THE PRO-COOPERATIVE HYPOTHESIS

Canid Success

This essay was prompted by the question of whether monogamy is a cause, consequence, or correlate of Canidae success, as individuals, species and family. Unlike many other carnivore families, canids have thrived in the rapidly changing conditions of the Anthropocene (Wang et al., 2007; Wang and Tedford, 2008). The world's most widely distributed wild terrestrial mammal is a canid: the red fox, found from the Arctic Circle to North Africa, North America and Eurasia and introduced and now widespread in Australia and USA (Macdonald and Sillero-Zubiri, 2004). Prior to the ascent of red foxes, this title was held by another canid, the gray wolf, originally distributed throughout the Northern Hemisphere in every habitat large ungulates were found (Mech, 1995; Macdonald and Sillero-Zubiri, 2004), until widespread human persecution caused their near-complete extirpation by the late 1800s (Mech, 1995; Phillips et al., 2004). But canids are resilient and gray wolves are now returning to their former range in both North America and Europe (Mech, 1995, 2017; Breitenmoser, 1998; Wydeven et al., 1998; Phillips et al., 2004). Coyotes have dramatically increased their range over the past two centuries. Previously found only in the prairies and deserts of western North America, they are now ubiquitous in every country and state from Alaska to Panama, found in nearly all available habitats, including forest, prairie, desert, mountain, tropical habitats, and cities (Gompper, 2002; Macdonald and Sillero-Zubiri, 2004). Coyote range expansion was likely catalyzed by the extermination of gray wolves, thus reducing intra-guild competition (Macdonald and Sillero-Zubiri, 2004), and land conversion through logging and agriculture which opened up additional habitat (Méndez–Carvajal and Moreno, 2014). The rapid expansion of coyotes in North and Central America is mirrored by that of golden jackals in Europe. Native to the Middle East and southern Asia, golden jackals arrived at the southern edge of Central and Eastern Europe around 8,000 years ago and began slowly expanding in the nineteenth century, but since the 1950's their expansion has accelerated into the north and west of Europe (Tóth et al., 2009; Rutkowski et al., 2015). They are now found as far north as Finland, four degrees below the Arctic Circle (Banea and Giannatos, 2019), and as far west as Switzerland (Arnold et al., 2012; Trouwborst et al., 2015) and their continued expansion, for reasons paralleling those for coyotes, seems likely (Arnold et al., 2012). In addition to these natural rapid expansions, introductions of canids by humans allowed several to thrive as invasive species. Raccoon dogs, originally from Siberia, East Asia and Japan, were introduced as a furbearing species in the Soviet Union from 1928 to 1955 and within 50 years had colonized 1.4 million km^2 of northern and eastern Europe (Helle and

Kauhala, 1991; Kauhala and Saeki, 2004; Sutor, 2007; Kauhala and Kowalczyk, 2011). The reintroduction and subsequent rapid spread of red foxes in mainland Australia and USA is another classic example of biological invasion (Kamler and Ballard, 2002; Fleming et al., 2006). The domestic dog, a few genes adrift from gray wolves, is one of the world's most successful mammal: population estimates range from 700 million (Hughes and Macdonald, 2013) to over one billion (Lord et al., 2013), roughly 80% of which are estimated to be free-ranging (Lord et al., 2013). Despite considerable efforts, humans have been unable to control the populations of these canids.

What has allowed these canids—red fox, gray wolf, coyote, golden jackal, raccoon dog, and domestic dog—to be so successful as to rapidly colonize new areas, dramatically increase in abundance, and continue to do so despite human efforts to control populations, and could their monogamous lifestyle be partially to blame? We suggest that canid success may be attributed to four main characteristics: (1) their generalist nature, adaptability, flexibility, and intelligence, allowing them to adapt to diverse habitats, diets and circumstances; (2) their high mobility and capacity for long-distance travel, facilitating fast colonization, expansive gene flow and genetic diversity, creating a selective advantage in changing environments and minimizing the risk of inbreeding from founder effects (Reed and Frankham, 2003); (3) their high reproductive rate, allowing them to quickly increase in number and recover following population declines from disease and persecution; and (4) their sociality and ability to cooperate, which can provide numerous benefits (see section Ecological Correlates of Social Monogamy: Social Structure; Macdonald and Carr, 1989; Macdonald et al., 2004). We argue that while the first and second attributes on this list are conserved traits that arose early in canids' phylogenetic history, the third and fourth are consequences of monogamy, and that it is the combination of these four characteristics that contribute to canids' success.

Canid Success Traits That Are Consequences of Monogamy
High Reproductive Rates
Co-evolution of paternal care and litter size resulted in the large litters that are characteristic of canids, thus increasing reproductive output (Stockley and Hobson, 2016). Canids can also reproduce in their first year and breed annually (Lord et al., 2013). In comparison to other omnivorous Carnivores, canids are distinguished by the platform provided by monogamy for benefiting from paternal care, cooperative breeding and allopaternal care, all of which can enhance lifetime reproductive success (Lukas and Clutton-Brock, 2013; Opie et al., 2013). Rapid reproduction allows canids to withstand high mortality rates (from human persecution and disease, itself often anthropogenic; Goltsman et al., 1996; Laurenson et al., 1998; Rhodes et al., 1998) and quickly colonize new areas. Despite widespread persecution, red foxes, coyotes, golden and black-backed jackals and raccoon dogs are able to thrive, while wolves continue to recover in North America and Europe despite ongoing illegal killings (Mech, 1995, 2017).

High reproductive rates may also allow for rapid phenotypic and genotypic adaptations to cope with new or changing environments and prevents inbreeding depression (Reed and Frankham, 2003). Furthermore, socially monogamous mating systems are predicted to produce greater reproductive output and genetic diversity compared to polygynous or polyandrous systems, leading to larger effective population sizes (Parker and Waite, 1997; Waite and Parker, 1997).

Sociality and Cooperation
The complex, cooperative social systems of canids that evolved from monogamy (Lukas and Clutton-Brock, 2013; Dillard and Westneat, 2016) provides numerous benefits discussed in section Canid Social Monogamy (e.g., cooperative hunting, food defense, reproductive success). Furthermore, the cooperation that first developed between members of the monogamous pair can spill over to other individuals, generally kin, when resource dispersion facilitates cohabitation by a spatial group (see Macdonald and Johnson, 2015). While this might originally be focused on young, it is a small step to cooperating with, and even assisting, other adult group members (e.g., adult red foxes caught in traps may be fed by other foxes [Garcelon et al., 1999]).

Canids have among the largest relative brain sizes in Carnivora (Gittleman, 1986; Swanson et al., 2012) and an enlarged pre-frontal cortex compared to felids and other carnivores (Rakinsky, 1969), associated with increased intelligence and behavioral complexity and flexibility. Across carnivore species, experiments show that greater relative brain size is associated with greater problem solving (Benson-Amram et al., 2016) and across mammals, larger brain sizes are associated with the ability to successfully adapt to, colonize, and invade novel habitats (Sol et al., 2008). The sociality and cooperation that evolved in canids from monogamy may have increased canid brain size through influence on diet. Cooperative hunting allows canids to tackle larger vertebrate prey and increases hunting success (Fanshawe and Fitzgibbon, 1993; Creel and Creel, 1995). Carnivore species that consume vertebrates have the largest brains, omnivores intermediate, and insectivores the smallest (Swanson et al., 2012). This could be because hunting vertebrate prey is more cognitively demanding than omnivory or insectivory, and particularly when synchronizing hunting behavior with pack mates, or because consuming higher-energy foods allows evolution of metabolically expensive brain tissue (Swanson et al., 2012).

Increased brain size is also argued to be a consequence of the complex social relationships that monogamy requires. Shultz and Dunbar (2007) found that larger relative brain size is correlated with socially monogamous pair bonding in Carnivora, other mammalian orders, and birds. Furthermore, bird species with long-term monogamous pair bonds (like that of most canids) have larger brains than species with short-term seasonal monogamy (Shultz and Dunbar, 2007; West, 2014). Shultz and Dunbar (2010) concluded that increased brain size evolved in birds as a result of long-term pair bonding, not that larger brains allowed long-term pair bonding. Three hypotheses have been proposed for why monogamous pair bonding may select for larger brains. Shultz and Dunbar (2007) and Dunbar (2009)

argue that the cognitive demands of behavioral coordination, synchronization, and negotiation necessary for navigating and maintaining stable pair bonded partnerships is responsible for increased brain sizes seen with monogamy. Alternatively, the potentially high costs of selecting an unreliable or infertile mate, particularly in species forming long-term monogamous pair bonds where there is reduced availability of alternative mates, may have selected for cognitively-demanding mate selection processes (Dunbar, 2009). A third hypothesis relates to the pressures of mate guarding and procuring fitness-increasing extra-pair copulations while maintaining social partnerships (West, 2014). This is supported in birds, where larger brains not only correlate with social monogamy but also with extra-pair paternity: as rates of extra-pair paternity increase, so does brain size. This suggests there is an intersexual co-evolutionary arms race with both sexes trying to outsmart each other in trying to sneak extra-pair copulations while preventing their mate from doing the same, leading to larger brains in both sexes (West, 2014).

Sociality beyond the pair bond may also contribute to increased brain sizes. Swanson et al. (2012) found that carnivoran social complexity is positively correlated with relative cerebrum volume (but not total brain volume), in line with the social brain hypothesis in primates which posits that larger brains evolved due to the cognitive demands posed by complex social systems (Dunbar, 1992; Shultz and Dunbar, 2007; but see DeCasien et al., 2017) (studies on the relationship between total relative brain volume and carnivore sociality have found conflicting results, see Gittleman, 1986; Dunbar and Bever, 1998; Pérez-Barbería et al., 2007; Shultz and Dunbar, 2007; Finarelli and Flynn, 2009; Swanson et al., 2012).

Thus, the sociality and cooperation that evolved in canids as a result of monogamy also likely made them more intelligent and adaptable compared to other carnivore families, which would have further facilitated the relative dominance of canids and allowed several canid species to prosper even during the Anthropocene.

In this sense, monogamy primed pro-cooperative, pro-social behaviors in ancestral canids that were, and largely remain, facultative rather than obligate. This facility for cooperation offers canids a selective advantage to maximize opportunities more readily than would have been the case without the pro-cooperative bonus brought by monogamy.

Conserved Traits for Success Amongst the Canidae
Intra-Specific Ecological Flexibility
Canids are highly flexible and adaptable in their ecology, able to exploit a wide range of diets, habitats, and social structures. Although the central theme of canid social and mating systems is monogamy, their extreme flexibility leads to intraspecific variation in social behavior as adaptations to varying ecological conditions, allowing them to take advantage of superior strategies when opportunity permits. Consider the finding of Robertson (2016) that in areas with low resource availability, female coyotes delay reproduction and instead bide at home as helpers, more

than half breeding only after their third year. In areas with high resource availability, almost half bred as yearlings, and almost all did so by their third birthday. This flexibility allows rapid increases in numbers, contributing to resilience to intense hunting pressure (Berger, 2006). Interspecifically, consider the domestic dog, which abandoned the *Canis* pattern of monogamy and its associated social and reproductive traits to take advantage of the abundant resources in its niche, allowing domestic dogs to become the most abundant carnivore on earth (Hughes and Macdonald, 2013; Lord et al., 2013). The remarkable intra-specific flexibility of canids means that while monogamy, and the cooperation it facilitates, is their norm, they can survive and even sometimes thrive alone when needed (much like omnivorous viverrids and musteloids) or adopt polygamy when ecological conditions present that as a superior strategy. They can be flexible as necessity or circumstance requires or permits.

High Mobility
Canids are capable of fast and wide-ranging movements. Movements of 86 km in a little over a month and 230 km in ~3 months have been recorded in the African golden wolf (Karssene et al., 2018), gray wolves disperse as far as 1,000 km in search of new territories and mates (Mech et al., 1995; Ciucci et al., 2009) and minimum dispersal distances documented for coyotes are 94 km for females and 113 km for males (Harrison, 1992). The interplay of this high mobility with their ecological flexibility allows canids to quickly move to new areas and adjust to local conditions.

Formula for Canid Success: the Monogamy as Pro-cooperative Hypothesis
The four attributes presented above may be the keys to the formula of canid success among carnivores. This hypothesis might be termed the *monogamy as pro-cooperative hypothesis* (**Figure 1**). In short, monogamy appears to have arisen when females are dispersed between sharable territories that arise as a result of the dispersion of available resources (Macdonald and Johnson, 2015), preventing males from defending multiple females but nonetheless allowing them to cohabit with one, such that guarding a single female is the most efficient male strategy (Komers and Brotherton, 1997; Brotherton and Komers, 2003; Lukas and Clutton-Brock, 2013), emerging from the ancestral canids' ecological circumstances. Monogamy together with biparental and alloparental care allowed for high reproductive output and cooperative sociality and intelligence. This perspective is congruent with Lukas and Clutton-Brock (2013) conclusion, based on phylogenetic analysis, that biparental care evolved from social monogamy, and cooperative breeding systems evolved from that. Their high mobility allows canids to quickly expand to new areas, their intelligence and generalist nature allows them to adapt to new diets and habitats in these new areas, and together with their high reproductive output and cooperative sociality allows them to quickly increase in numbers and successfully colonize.
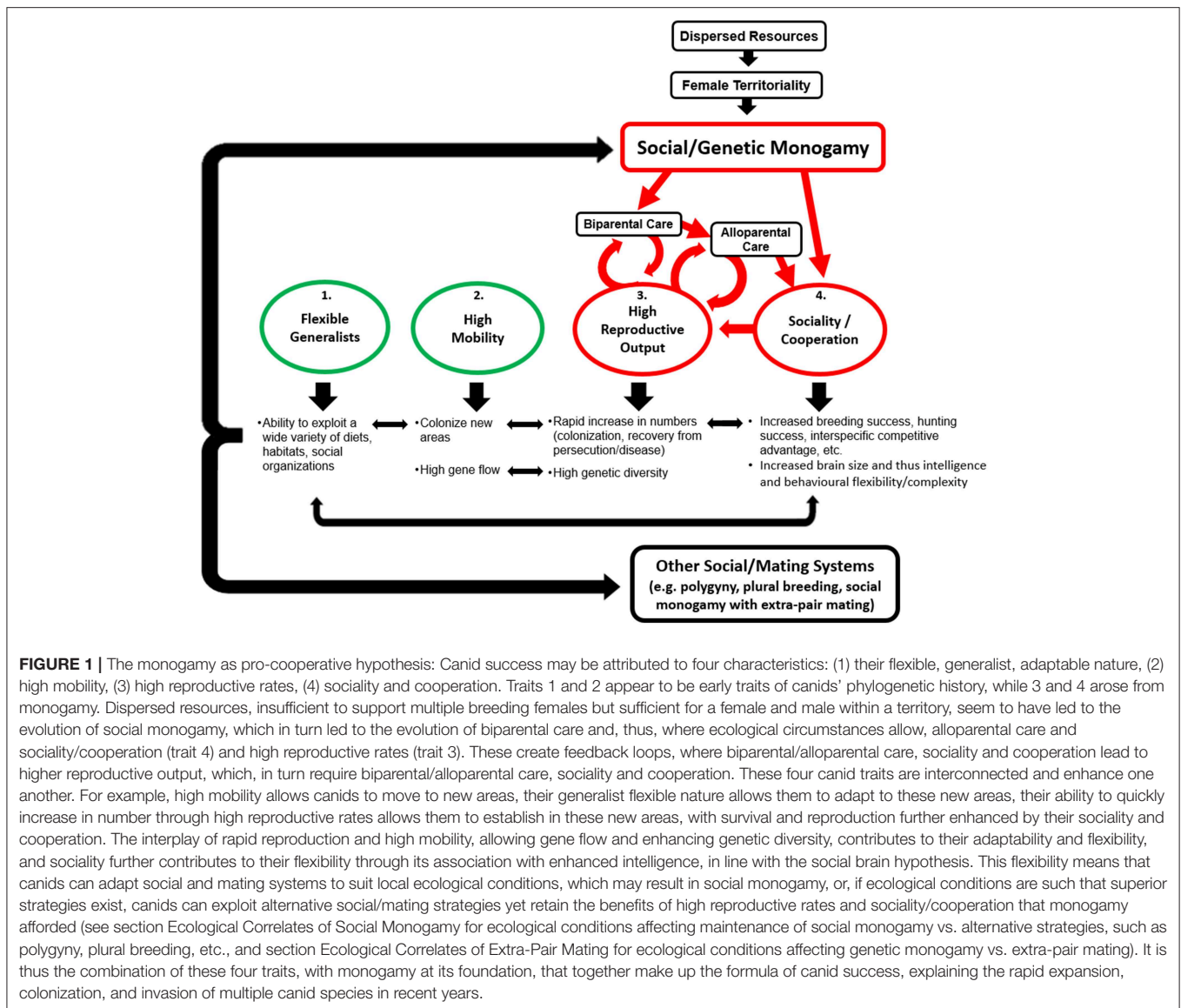
FIGURE 1 | The monogamy as pro-cooperative hypothesis: Canid success may be attributed to four characteristics: (1) their flexible, generalist, adaptable nature, (2) high mobility, (3) high reproductive rates, (4) sociality and cooperation. Traits 1 and 2 appear to be early traits of canids' phylogenetic history, while 3 and 4 arose from monogamy. Dispersed resources, insufficient to support multiple breeding females but sufficient for a female and male within a territory, seem to have led to the evolution of social monogamy, which in turn led to the evolution of biparental care and, thus, where ecological circumstances allow, alloparental care and sociality/cooperation (trait 4) and high reproductive rates (trait 3). These create feedback loops, where biparental/alloparental care, sociality and cooperation lead to higher reproductive output, which, in turn require biparental/alloparental care, sociality and cooperation. These four canid traits are interconnected and enhance one another. For example, high mobility allows canids to move to new areas, their generalist flexible nature allows them to adapt to these new areas, their ability to quickly increase in number through high reproductive rates allows them to establish in these new areas, with survival and reproduction further enhanced by their sociality and cooperation. The interplay of rapid reproduction and high mobility, allowing gene flow and enhancing genetic diversity, contributes to their adaptability and flexibility, and sociality further contributes to their flexibility through its association with enhanced intelligence, in line with the social brain hypothesis. This flexibility means that canids can adapt social and mating systems to suit local ecological conditions, which may result in social monogamy, or, if ecological conditions are such that superior strategies exist, canids can exploit alternative social/mating strategies yet retain the benefits of high reproductive rates and sociality/cooperation that monogamy afforded (see section Ecological Correlates of Social Monogamy for ecological conditions affecting maintenance of social monogamy vs. alternative strategies, such as polygyny, plural breeding, etc., and section Ecological Correlates of Extra-Pair Mating for ecological conditions affecting genetic monogamy vs. extra-pair mating). It is thus the combination of these four traits, with monogamy at its foundation, that together make up the formula of canid success, explaining the rapid expansion, colonization, and invasion of multiple canid species in recent years.

Comparison Within Canidae

To consider further the role these four traits play in canid success, we explore how some of the most successful wild canids, as outlined above—red fox, golden jackal, coyote, raccoon dog— differ from those species that are not faring so well. Of the 37 extant Canidae species, one is listed by the IUCN as Critically Endangered (red wolf) and four as Endangered (Ethiopian wolf, African wild dog, dhole and Darwin's fox); no species are listed as Vulnerable and only one canid has gone extinct in historical times (Falkland islands wolf, *Dusicyon australis*, in 1876). How do these species differ? For the Falkland islands wolf and Darwin's fox, their small and isolated ranges, was and is their main downfall. For the other species mentioned here, they lack a critical piece of the puzzle for canid success—their generalist, adaptable nature. African wild dogs and dholes are hypercarnivorous, with specialized dentition for a diet primarily of large vertebrate prey.

Their large body size coincides with high energy requirements (Carbone et al., 1999; Slater, 2015), meaning they must consume large prey for foraging to be energetically economical. This results in a greater reliance on cooperative hunting, such that, unlike other canids that can adjust social structure and thrive alone, as pairs, or in groups, these species may have a minimum pack size threshold for successful hunting and breeding (Carbone et al., 1999). The African wild dog and dhole are also among the least monogamous canids—dholes tend to exhibit communal breeding, living in large clans and more often with multiple breeding females in a group (Fox, 1984), while African wild dogs are often polyandrous or polygynandrous with multiple litters in a pack (see section Ecological Correlates of Extra-Pair Mating). African wild dogs deviate from other canid patterns—they exhibit the shortest recorded post-copulatory lock (Frame et al., 1979; Asa and Valdespino, 1998), which we

suggested could be a monogamy enforcement adaptation (section Post-copulatory Lock). The Ethiopian wolf has also increased dietary specialization, but in the opposite direction—rather than specializing on large prey, this species specializes on Afroalpine rodents, which can comprise as much as 97% of prey volume of their diet (Sillero-Zubiri and Gottelli, 1995b). Afroalpine rodent communities can therefore limit the distribution of Ethiopian wolves (Sillero-Zubiri et al., 1995a,b).

Comparison Among Carnivora

To isolate the importance of monogamy within the canid syndrome of breeding fast and cooperating as opportunity allows requires solving the algebra of alternative evolutionary pathways that led other generalist, omnivorous carnivores to life histories that do not involve monogamy. How do they fare?

Consider the feliform solution to the same evolutionary problem, the Viverridae (genets and civets). Although viverrid biology is not well-known (e.g., Ross et al., 2017) they too excel at omnivory, but exhibit classic carnivorean polygyny, produce small litters, and lack the pioneering adaptability and cooperative tendencies of canids. The same might be said of most omnivorous musteloids and ursids, themselves carrying much of the caniform phylogenetic baggage shared by canids (Koepfli et al., 2017), but with societies conspicuously lacking monogamy (Macdonald and Newman, 2017). The comparison is not flawless, but sufficiently compelling that the role of monogamy in the syndrome of canid attributes is part of their particular success. Perhaps the extinction of the tenth family of caniforme Carnivores, the Amphicyonidae (the "bear-dogs"), 2.6 million years ago, probably due to competition with true dogs, lay in the trump card of monogamy. The point might even be stretched to explain how, five million years ago, canids ousted the dog-like Hyeanidae that once outnumbered them (Macdonald, 1992). Amongst the Caniforme suborder of Carnivora, despite

their close phylogenetic relationships, Canidae are the only family to exhibit monogamy. Of the 37 extant canid species, only 5—13.5%—are listed as threatened (Critically Endangered, Endangered, or Vulnerable) on the IUCN Red List. This is the lowest proportion among all Caniforme families. An avenue worth exploring may be associations between the conservation status of species in a family and the number of the critical traits identified here that they exhibit (amongst Caniforme families we think that none other than canids display all four).

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