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Variation in reproductive traits of members of the genus *Canis* with special attention to the domestic dog (*Canis familiaris*)

Kathryn Lord[a,*], Mark Feinstein[a], Bradley Smith[b], Raymond Coppinger[a]

[a] *Hampshire College, School of Cognitive Science, Amherst, MA 01002, USA*
[b] *Central Queensland University, Appleton Institute, 44 Greenhill Road, Wayville, South Australia 5034, Australia*

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ABSTRACT

We compare differences in the reproductive strategies of "free-living" dogs with their wild relatives in the genus *Canis*, of which the dog is a very recently evolved member. The members of this genus display a greater range of parental motor patterns than generally seen in other species of *Carnivora*, including pair-bonding and extended parental care; parents regurgitate to offspring and provision them with food for months to as long as a year. But the domestic dog does not routinely display these genus-typical behaviors. While this has generally been assumed to be a result of direct human intervention, humans have little reproductive control over the vast majority of domestic dogs. We analyze the low frequency of display of genus-typical behaviors and postulate that the dog's reproductive behaviors are an adaptation to permanent human settlement and the waste resources associated with it. Adaptation to this environment has decreased seasonality, increased the fecundity of unrestrained dogs and reduced the need for prolonged parental care. The consequences of greater fecundity and reduced parental care are compared to the reproductive behavior of other species of the genus.

Contents

* Corresponding author.
E-mail address: klord3@me.com (K. Lord).

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1. Introduction

The genus *Canis* includes six incipient (inter-fertile) species: the dog (*C. familiaris*), the wolves (*C. lupus* and *C. simensis*), coyotes (*C. latrans*), jackals (*C. aureus*), and dingoes (*C. dingo*). There are two other members of the genus, the black-backed jackals (*Canis mesomelas*) and side-striped jackals (*C. adustus*) that are more distantly related and probably not interfertile with the others included in our review. We understand that there is an ongoing discussion of the nomenclature and classification of the current members of the genus (see Coppinger et al., 2010, for a review).

The members of this genus exhibit reproductive behaviors not commonly found in the *Carnivora* or even other *Canidae*. African hunting dogs (*Lycaon pictus*) and several species of the South American genus *Pseudalopex* (Muñoz-Donos, pers. com.) are reported to have similar parental behaviors, but they are not inter-fertile with the domestic dog, which is our central concern. We have focused our discussion on differences in seasonality and parental behavior within the genus *Canis*, noting that the dog is atypical.

The worldwide population of *C. familiaris* is unknown and difficult to calculate. One estimate is that there is approximately 1 dog for every 10 people (Wandeler et al., 1993), resulting in a figure of 700,000,000 dogs worldwide. This ratio varies dramatically regionally and Jackman and Rowan (2007) suggest that it is a relatively conservative figure. Alternatively, if we extrapolate from available calculations for individual countries (Rowan, pers. com.), based on landmass, we reach a figure of 1 billion dogs worldwide. If one assumes that all of the pet dogs in developed countries are restricted they would represent 17–24% of the dogs worldwide (Table 1). This is most likely an over-estimation of restricted dogs. A survey by New et al. (2004) suggests that over 50% of litters born to U.S. households are unplanned.

Thus, dogs that are not reproductively restrained comprise a naturally breeding population making up as much as 83% of the world's billion dogs. These dogs are clustered in areas of human waste such as discarded food or food by-products, carcasses, kitchen wastes, fecal material or even corpses (Butller and du Toit, 2002; Daniels and Bekoff, 1989; Oppenheimer and Oppenheimer, 1975; Wandeler et al., 1993; R.C., pers. obs.). In many areas of the world concentrations of 700–1000 or more freely reproducing dogs/km^2 are common around dumps, slaughterhouses, fishing ports, markets and other food processing and distributing areas (see Beck, 2000; Hsu et al., 2003; Reece, 2005; WHO, 2004, for examples). There is no evidence to suggest that humans have ever had control over the reproductive behavior of the vast majority of dogs, other than by culling. Consequently, it is plausible to think that any differences in reproductive behavior might be adaptations to a niche created by permanent settlement of humans and its associated waste products (Zeuner, 1963; Tchernov and Valla, 1997; Coppinger and Coppinger, 2001), and not by artificial selection as first claimed by Darwin (1858).

In the following sections we review the literature on three general features of reproductive activity in *Canis* (reproductive seasonality, age of first reproduction, and pair-bonding), and compare three feeding behaviors (nursing, regurgitation, and provisioning). We analyze the low frequency of display of genus-typical behaviors in the dog and postulate that the dog's reproductive behaviors are an adaptation to permanent human settlement and the waste resources associated with it, an issue that should not