Canid Reproductive Biology: an Integration of Proximate Mechanisms and Ultimate Causes[1]

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SYNOPSIS. The canid reproductive system includes many features that are unusual or even unique among mammals. Focusing on gray wolves, for example, these include monogamy, monestrum with exceptionally long proestrous and diestrous phases, a copulatory lock or tie, incorporation of adult young into the social group, behavioral suppression of mating in these subordinate young, obligate pseudo-pregnancy in subordinate females, and alloparental care. These features can be analyzed on the levels of both proximate and ultimate causation by considering them in the context of the reproductive system as a whole. First, when assessing possible proximate mechanisms, monestrum appears to be pivotal. It is probably accomplished by the extremely long luteal or diestrous phase, which is followed by a seasonal peak in prolactin. Two sequellae of the extended diestrus (or pseudo-pregnancy) in non-pregnant subordinate females are to 1) suppress any subsequent cycles, and 2) hormonally prime them to behave maternally. The prolactin peak in all adult pack members, coincident with the birth of pups, also may stimulate parental behavior. The risk of monestrum (limited chance for conception) appears to be reduced by the relatively long proestrous and estrous periods, as well as by monogamy. The adaptive value, or ultimate cause, of this reproductive system is most obvious for the more social canid species, such as the gray wolf. That is, advantages to sociality, such as cooperative hunting, may have driven development of the anomalies of the reproductive system.

INTRODUCTION

In reviews of mammalian reproductive systems, canids are most often cited as being unusual because they exhibit monogamy and paternal care (e.g., Kleiman, 1977). However, other uncommon and even unique features characterize this group, including monestrum with exceptionally long proestrous and diestrous phases, a copulatory lock or tie, incorporation of adult young into the social group, behavioral suppression of mating in these subordinate young, obligate pseudopregnancy in subordinate females, and alloparental care (Asa, 1996). There has been considerable discussion about the social organization of canids in regard to ultimate causation of reproductive systems, e.g., helping behavior, group size, and even monogamy (see Kleiman and Eisenberg, 1973; Kleiman, 1977; Kleiman and Malcolm, 1981; Moehlman and Macdonald, 1983; Moehlman, 1986; Geffen et al., 1996). However, little attention has been paid to proximate causation. Data on reproductive endocrinology and morphology, especially if integrated with information from behavioral studies, can provide a broader understanding of reproductive strategies and even of ultimate causation.

Because there are extensive data on both its reproductive physiology and social interactions, the gray wolf (Canis lupus) presents a convenient example to begin an evaluation of the interplay between these systems.

THE GRAY WOLF

The typical gray wolf pack is a family unit headed by a dominant, breeding pair and their subordinate young, some of whom may be post-pubertal (Mech, 1970). The timing of dispersal probably depends on lo-

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cal conditions such as the density of prey and of other wolves. New packs are formed by dispersing wolves that pair and produce young, though new genetic data suggest that occasionally new wolves are incorporated into an existing pack (Gompper and Wayne, 1996). Breeding is strictly seasonal, with increases in territorial scent-marking by the dominant male and in testosterone in all adult males beginning in the fall (Asa *et al.*, 1990). All adult pack members, even males, may guard and play with pups and provision both mother and pups.

Puberty usually occurs at 22 months of age in both males and females, as defined by first sperm production and first ovulation, respectively. Under some circumstances, such as the death of the dominant female, first estrus may occur a year earlier (Seal *et al.*, 1979). However, as long as young adults remain subordinate in their natal group, mating and reproduction typically are delayed. The suppression of reproduction is behavioral, though, not physiological (Packard *et al.*, 1983, 1985).

The stages of the ovulatory cycle are longer than for most other mammals. The mean length of proestrus is approximately six weeks and that of estrus about one week (Asa *et al.*, 1986). Proestrus is accompanied by gradually increasing estradiol that stimulates a sanguinous uterine discharge beginning in late fall/early winter. The spontaneous ovulation is preceded by a rise in progesterone that, together with estradiol, initiates estrus, the receptive phase, in all post-pubertal females regardless of rank (Seal *et al.*, 1979).

The luteal or diestrous phase that follows ovulation is remarkably long, lasting for a time equivalent to pregnancy, about two months, and for this reason is sometimes called pseudopregnancy. Not only is progesterone elevated in all females that ovulate, but no other hormonal differences have been found between pregnant and pseudopregnant females (Seal *et al.*, 1979; Asa *et al.*, 1986; Kreeger *et al.*, 1991).

Gray wolf reproduction is strictly seasonal, which is not unusual for a temperate zone species. However, the restriction of seasonal reproduction to only one ovulatory cycle, or monestrum, is indeed rare. Po-

lyestrum, typical of most other mammals, is characterized by successive cycles of estrus and ovulation without any intervening period of anestrus (reproductive quiescence) and can be either seasonal or continue year round. Thus, if a polyestrous female fails to conceive at one ovulation, she will have additional opportunities. In contrast, female wolves have only one estrus and so only one chance to conceive per season.

The proximate cause of monestrum may be the obligatory extended luteal phase that follows the annual ovulation. In the typical polyestrous ovarian cycle, elevated luteal phase progesterone is associated with suppression of ovulation. The final growth of ovulatory follicles is prevented until progesterone levels decline, which then allows initiation of the follicular phase and ovulation of the next cycle. The mechanism in the wolf seems to be similar but is extended due to the long life of the corpus luteum (CL), the ovarian structure responsible for progesterone synthesis and secretion. It appears that by the time the CL recedes, the seasonal window for renewed ovarian activity in the gray wolf is closed.

The length of the breeding season may be limited by the annual spring increase in prolactin, a pituitary hormone that can inhibit gonadotrophins and gonadal steroids (see Greenwald and Terranova, 1988). In gray wolves, all adult animals, even gonadectomized individuals, experience a seasonal peak in prolactin in the spring (Kreeger *et al.*, 1991).

Although the proximate cause for monestrum may be the very long-lived CL, the ultimate cause may be related to social system. First, it eliminates the chance for additional periods of estrus in subordinates that might cause social dissention. If wolves were polyestrous, the dominant female would likely conceive on the first or at least the second cycle, but as long as subordinates were prevented from mating they would continue to cycle. The repeated periods of estrus in subordinates, necessitating behavioral intimidation or perhaps even physical aggression by the dominant animals, would undoubtedly strain the cohesiveness of the pack.

Still, monestrum seems a reproductively

very risky strategy, in that only one ovulatory event occurs during each breeding season. However, that risk is probably reduced by the lengthy proestrus and estrus. It is likely that the chances for conception are enhanced by the additional time the wolf pair spends coordinating their activity. During proestrus they spend much time together and repeatedly perform double-urine-marking, a behavior that appears important to the formation and maintenance of the pair bond (Mech and Knick, 1978; Rothman and Mech, 1979; Asa et al., 1986, 1990). Also, the relatively long period of estrus provides time for more copulations.

The relationship between monestrum and the extended luteal phase, or pseudopregnancy, involves still another aspect of female gray wolf behavior. Because of the endocrine similarity to pregnancy, all females that ovulate are then hormonally primed to show maternal behavior. Some may even lactate. The potential benefit of this helping behavior to the pack is obvious.

The hormonal priming provided to subordinate females by pseudopregnancy, though, does not explain the parental care exhibited by male pack members. However, the seasonal increase in prolactin may provide the proximate cause, since its peak coincides with the birth of pups (Kreeger et al., 1991). Although its involvement in parental behavior in gray wolves or other canids has not been experimentally established, prolactin has been associated with paternal as well as maternal behavior in other species (for review, see Bridges, 1990; and Brown, 1993). Yet, even if prolactin does stimulate parental care in gray wolves, its annual rhythm is probably driven by changes in photoperiod, as has been documented for many other species.

Some features of this system, such as monestrum, monogamy, and delayed reproduction, might at first seem to diminish lifetime reproductive success. However, they may be important in relation to aspects of gray wolf social system. The benefits of monestrum have already been discussed, and it is likely related in some ways to monogamy, since the continued or seasonal presence of the same male would make monestrum less risky. Monogamy may also be

related to paternal investment, as is common in other species (Trivers, 1972). That is, a male is more likely to invest in young if he can be certain he is their sire. The continued association of a monogamous pair increases the likelihood of paternal investment.

It is likely that the advantages of delayed reproduction in non-dispersing subordinates are similar to those in other species, i.e., inclusive fitness that is higher than or at least equal to that which would accrue to a disperser under similar conditions. For wolves, the degree of relatedness of the non-disperser to its younger siblings is equal to its potential relatedness to its own offspring since monogamy ensures that both parents are shared by all siblings, even those of successive years. Thus, a young wolf may actually leave more genes in a given year by remaining in its natal pack if its prospects for reproduction outside the pack are not good.

In some primates such as the common marmoset, Callithrix jacchus jacchus (Abbott et al., 1981), subordinate reproduction also is delayed, but by physiological suppression, i.e., puberty is delayed in offspring that do not disperse. For the gray wolf, though, behavioral rather than physiological suppression of reproduction in subordinate females may be preferable since ovulation results in obligate pseudopregnancy that may facilitate maternal behavior. However, if seasonal increases in prolactin stimulate parental behavior in males, it is not clear why prolactin would not also be sufficient to support parental behavior in females.

Another feature of wolf reproductive behavior, the copulatory tie, is probably also related to sociality. As long as the dominant male remains intromitted, no other pack member can gain access to the female during the period of sperm transport (see Dewsbury, 1978), which may be especially important if the post-ejaculatory male is less alert.

OTHER CANIDS

Monogamy

An obvious question is whether the picture that emerges for the gray wolf applies

TABLE 1. *Categories of male parental investment in the family Canidae.*

	Groom	Carry	Provide food	Defend	Baby sit	Play	Guard	Care to female
Gray wolf								
Canis lupus			+	+	+	+	+	+
Red wolf								
C. rufus			+				+	
Coyote								
C. latrans			+	+	+	+	+	+
Golden jackal								
C. aureus			+	+	+	+	+	+
Black-backed jackal								
C. mesomelas			+	+	+	+	+	+
African wild dog								
Lycaon pictus	+	+	+	+	+	+	+	+
Dhole								
Cuon alpinus			+	+				+
Arctic fox								
Alopex lagopus			+			+		+
Red fox								
Vulpes vulpes			+					+
Cape fox								
V. chama			+					
Corsac fox								
V. corsac				C				
Kit fox								
V. macrotis			+					
Swift fox								
V. velox			+					
Fennec fox								
Fennecus zerda			+				C	C
Raccoon dog								
Nyctereutes procyonoides								C
Bat-eared fox								
Otocyon megalotis			+		+	+	+	+
Andean fox								
Dusicyon culpaeus			+					
Pampas fox								
D. gymoncercus			+					
Crab-eating fox								
Cerdocyon thous			C	C	C			C
Maned wolf								
Chrysocyon brachyurus				C				
Bush dog								
Speothos venaticus			C	C	C	C		

Field: +, captivity: C; Modified from Kleiman and Malcolm, 1981; References in Asa, 1996.

to other canids as well. Indeed, the modal reproductive pattern for canids is similar to that of wolves and includes: monogamy (except under particular circumstances; see Lott, 1984; Zabel and Taggart, 1989) with paternal care (Table 1; Kleiman and Malcolm, 1981; Asa, 1996); large, altricial litters (mode: 3 to 6: Hayssen *et al.*, 1993); and one litter per year. The crab-eating fox, *Cerdocyon thous*, and bush dog, *Speothos venaticus*, are exceptions in that they are reported to have two litters per year in cap-tivity (Brady, 1978; Porton *et al.*, 1987), as does the domestic dog (*Canis lupus familiaris*).

The occasional occurrence of polygyny in areas of overlapping female red fox (*Vulpes vulpes*) territories and very dense prey (*e.g.*, Zabel and Taggart, 1989; Macdonald, 1979), suggests that monogamy is less important to the female than is paternal care. When resources are very rich, a single male can adequately provision more than one female.

However, the presence of adult offspring in the natal group is not always associated with "helping" behavior. For example, in a study of gray wolves Harrington *et al.* (1983) found that older siblings fed pups only when prey density was high enough to result in surplus. Also, yearling Blanford's fox females (*Vulpes cana*) may remain on their parents territories but do not assist with subsequent litters (Geffen and Macdonald, 1992). This situation may perhaps be explained by the invertebrate food base of this species which may preclude efficient provisioning of young. If so, the parental role of males, who are reported to be strictly monogamous, may be focussed on guarding pups or maintenance of a feeding territory. Perhaps yearling females contribute to guarding and territory maintenance.

Monestrum

Although information is not available on every species, in surveys of canid reproductive systems (see Asa, 1996) several other characteristics appear to be common. All species for which there are data are monestrous (except the bush dog: Porton *et al.,* 1987), all species in which physiology has been studied have obligate pseudopregnancy, and incorporation of subordinate adults in the social unit is reported in at least some circumstances for most species (Table 2). These features appear most adaptive in the context of a family group such as gray wolves, African wild dogs (*Lycaon pictus*), coyotes (*C. latrans*), and black-backed (*C. mesomelas*) and golden jackals (*C. aureus*).

Yet, most other canids do not typically show that degree of sociality. Smaller species, such as the foxes with diets that rely on rodents and fruits, tend less toward sociality, probably because there is little or no benefit to group or cooperative hunting (see Creel and Macdonald, 1995). These species sometimes incorporate subordinate adult offspring into the parental social group (Asa, 1996), but this occurrence appears not to be common. Thus, the need for monestrum, for example, to minimize social disruption, and for obligate pseudopregnancy to ensure maternal behavior of subordinate females, is not clear for these species.

TABLE 2. *Canid species with monestrum, obligate pseudopregnancy and subordinate adult offspring in social unit.*

Monestrum	Obligate pseudopregnancy	Subordinate adult offspring
Gray wolf	Gray wolf	Gray wolf
Domestic dog	Domestic dog	Dingo
Coyote	Coyote	Red wolf
Arctic fox	Arctic fox	Coyote
Red fox	Red fox	Golden jackal
Kit fox	Andean fox	Black-backed jackal
Swift fox		
Andean fox		Arctic fox
Pampas fox		Red fox
Maned wolf		Blanford's fox
		Corsac fox
		Dhole
		African wild dog

Domestic dog: *C. lupus familiaris* or *C. familiaris*). Dingo (feral domestic dog): *C. lupus dingo* or *C. familiaris dingo*). Blanford's fox: *V. cana.* Scientific names of other species given in Table 1.

If the more social species such as the gray wolf represent the ancestral form upon which evolutionary pressures acted, these features might simply have been conserved in the less social species, perhaps maintained due to occasional benefit when conditions keep post-pubertal young from dispersing. However, current molecular and biochemical data suggest that a more fox-like canid was ancestral (Wayne *et al.,* 1989; personal communication by R. K. Wayne). Although it is not possible to know the degree of sociality of ancestral canids, modern foxes are considered less social than are gray wolves. However, the raccoon dog (*Nyctereutes procyonoides*) and bat-eared fox (*Otocyon megalotis*), that are thought to be more primitive forms along with the gray fox, have been shown to engage in more social interactions than the more recently derived foxes such as *Vulpes spp.* (Kleiman, 1967). If the more social raccoon dog and bat-eared fox do indeed represent the more ancestral form, then perhaps sociality was more important in the evolution of canid reproductive systems than would be suspected if *Vulpes*-like foxes are considered ancestral.

If, however, sociality is a more recently derived trait in the group-living gray wolf, dhole (*Cuon alpinus*), and African wild

dog, how might monestrum be adaptive, or at least not selected against? Although monestrum appears to limit chances for mating and conception, this might not actually be the case. For example, the very long proestrous and estrous periods may well compensate for the lack of additional cycles. First, the long proestrus increases the chances of locating a mate and/or establishing a pair bond. Furthermore, if total days of receptivity to mating are considered (mode 3 to 5 days), canids may well have as many opportunities to mate and conceive per season, on average, as polyestrous mammals with their typical one-day estrus per cycle with several cycles. Thus, overall, monestrum may not be a liability for the less social canids and may well provide important advantages to the social species.

Copulatory tie

Although of varying duration, a copulatory tie has been reported for all species in which copulation has been observed, even though it may be very brief in African wild dogs. It is possible, of course, that the tie serves only to enhance sperm and ovum transport, but it is tempting to posit a mate-guarding function to prevent sperm competition, as well (see Dewsbury, 1978). Yet, in the less social species mate-guarding should have less value. This is perhaps another attribute that argues for the ancestral canid to have been more social than the modern *Vulpes*-like foxes.

Seasonality

All temperate species of canids are strictly seasonal breeders. Although tropical species show more flexibility, most respond to prey cycles following seasonal rainfall. Because canids evolved in North America (Kurtin, 1971) where they would have been exposed to seasonal changes in daylength, it is reasonable to assume that their annual breeding cycle is driven by photoperiodic cues. This assumption is supported by the reports for three species translocated across the equator, in which breeding cycles shifted by six months (red fox, *V. vulpes*; and maned wolf, *Chrysocyon brachyurus*: Ewer, 1973; African wild dog: Cunningham, 1905). However, canids do not fall easily into the standard long-day or short-day breeding categories. For example, estrus in red foxes most often occurs in January and February in the Northern Hemisphere, but can be as early as December or as late as April (Sheldon, 1949; Kolb and Hewson, 1980). This means that proestrus (typically two weeks) may begin as late as March (increasing daylength) or as early as November (decreasing daylength). Furthermore, although photoperiod in mammals is considered to be mediated by the pineal gland, pinealectomy of gray wolves did not affect the occurrence or time of onset of any reproductive parameter in males or females (Asa *et al.*, 1987; Kreeger *et al.*, 1991).

Unlike most other canids, the approximately two monestrous periods per year in female domestic dogs are not seasonal (Christie and Bell, 1971). Male domestic dogs, presumably to be able to take advantage of any opportunity to mate, produce sperm year round, as do male dingoes (*C. lupus dingo*) in temperate regions of Australia (Taha *et al.*, 1981; Catling *et al.*, 1992). In other species in which females have a restricted breeding season, male reproductive physiology also varies seasonally (see Asa, 1996), that is, spermatogenesis is reduced or halted completely outside the breeding season.

African wild dogs are not strict seasonal breeders and are also unusual in having a sex bias favoring males. Thus, the typical pack contains many more males than females. It is interesting to speculate about whether the aseasonality and reduction in number of females in a pack might be related. The presence of subordinate females who might cycle at unpredictable times could increase social dissention and extend the time needed by the dominant female to prevent mating by these subordinates. Explanations for male bias have previously been attributed to possibly superior hunting abilities by males, but there is no evidence for a gender difference in hunting success (see Geffen *et al.*, 1996).

FENNEC FOX

Preliminary data from our ongoing study of reproduction in captive fennec foxes (*Fennecus zerda*) adds an interesting per-

spective, since it differs from the typical canid in several ways. As the smallest canid species, it does conform to some aspects of canid pattern in that it also breeds seasonally in the wild, producing one litter of one to three young once per year (Gauthier-Pilters, 1967). The litter is small and the young relatively precocial for a canid, which agrees with the pattern proposed by Moehlman (1986). In contrast, in captivity breeding appears not to be seasonal and there may be two periods of estrus per year (unpublished data, C.V. and C.S.A.). A further difference is that estrus with mating only lasts one to two days, and proestrus, based on vulval swelling, is also brief. Females appear to be monestrous, *i.e.*, a single ovulatory event is followed by an obligate endocrinological pseudopregnancy approximately equal in length to the 50- to 52-day gestation. However, based on preliminary data, we are not yet certain whether the species is truly monestrous (see Conaway, 1971 for an explanation of classifications). It is possible that the more frequent cycles should more accurately be termed polyestrous, if there is no anestrous period intervening between the end of pseudopregnancy (the long diestrous or luteal phase) and the subsequent proestrus, or between the end of lactation and the next proestrus. We hope to clarify the classification with further investigation.

Another extremely interesting feature of fennec reproduction is the relationship, at least in captivity, between male testicular activity and the female cycle. There is no apparent annual rhythm to the multiple estrous cycles, a pattern somewhat similar to the domestic dog. However, unlike male domestic dogs, cycles of testicular recrudescence in male fennecs appear to be synchronized with the monestrous cycles of their partners. That is, testis volume and sperm output vary during the year, with both parameters being elevated at the time of the female partner's period of estrus (unpublished data, C.V. and C.S.A.). Even more interesting is the possibility that testis activity declines following mating. In our colony, which is held under constant conditions of 12:12 light:dark, estrous cycles have not been synchronous. Thus, males do

indeed appear to be responding to some cue from the female (perhaps pheromonal), or the act of copulation may trigger hormonal events that result in the suppression of gonadal activity (see Brown, 1993).

It is not at first obvious why male fennecs would not remain spermatogenic year round like domestic dogs. In analyses of energetic investment, relative to female reproduction, sperm production is considered to be inexpensive (for example, see Lack, 1968). The answer for male fennec cyclicity may be related to paternal care. If the seasonal increase in prolactin is in fact a necessary proximate cause of paternal behavior in canids, species such as the fennec that do not reproduce in response to cues linked to seasonal changes in prolactin would be at a disadvantage. Instead, decreased aggression through decreased testosterone and concomitant elevations in prolactin to support paternal care may be accomplished in a different way. Studies are underway with fennecs to determine whether prolactin does indeed increase during the female partner's pregnancy, demonstrating an inverse relationship with testosterone.

CONCLUSIONS

Although there are many unusual features of reproduction common to canids, they may vary somewhat according to factors such as food abundance, body size, and degree of sociality. Overall, though, the adaptive value of physiological features, such as monestrum and obligate pseudopregnancy, is most evident in social species that incorporate adult offspring in the group. Unfortunately, hypotheses on the evolution of canid reproductive biology must be, for most species, based on very little data. Details of physiology are only available for a few, *e.g.*, gray wolf and farmed red foxes. Likewise, data from the field are extremely limited for many, especially bush dogs and many of the fox species. A more comprehensive analysis will require more information, especially on species that appear to deviate from the patterns that have emerged from currently available data.

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