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ASEASONALITY OF BUSH DOG REPRODUCTION AND THE INFLUENCE OF SOCIAL FACTORS ON THE ESTROUS CYCLE

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Temperate species of canids, both in captivity and in the wild, exhibit a rigid reproductive cycle with seasonal breeding and only one estrous period per year (Asdell, 1964; Ewer, 1973; Kleiman, 1968). Scattered accounts indicate that some tropical species of canids exhibit a greater degree of reproductive flexibility. *Lycaon pictus, cerdocyon thous,* and *Canis aureus* in tropical Asia, are reproductively aseasonal (Brand and Cullen, 1976; Frame et al., 1979; Nowak and Paradiso, 1983). *C. thous* (Brady, 1978) and *Speothos venaticus* (Kleiman, 1968) exhibit two estrous cycles per year, and *L. pictus* (Brand and Cullen, 1976; Frame et al, 1979) and *Fennecus zerda* (Koenig, 1970) have been reported to produce a second litter of pups within 6 months of losing the first.

The following observations of captive bush dogs (*S. venaticus*) suggest that this tropical canid posseses a more labile reproductive cycle than previously thought. Our research indicates that this species is aseasonal and occasionally polyestrous with the reproductive cycle influenced, in part, by social factors.

The main subjects of this study were five pairs of captive bush dogs whose identities and ages, pairing dates, social environment prior to pairing, and subsequent reproductive histories are presented in Table 1. The animals were housed in 4.9 by 10.4 m or 8.5 by 10.4 m outdoor yards, with access to 2.4 by 1.2 m indoor dens at the National Zoological Park's Conservation and Research Center (CRC) in Front Royal, Virginia. They were exposed to ambient temperatures and natural light cycles except during freezing temperatures, when they were locked indoors.

TABLE 1.—*The reproductive history of five pairs of bush dogs at the National Zoological Park's Conservation and Research Center.*

Individual history			Pair history					
Individual I.D.	Age at pairing (months)	Prior social condition	Pairing date	Estrous period (ties)	Interestrous interval (days)	Birth date	Interbirth interval (days)	Age of litter at removal from parents (weeks)
♂ 102669	9	with brother	28 Aug 1979	2 Sept 1979 (1)	5**			
♀ 102231	17	alone		21–24 Feb 1980 (*)	172	6 May 1980		40
				18–29 Dec 1980 (15)	297	4 March 1981	302	24
				28–30 June 1981 (5)	181	8 Sept 1981	188	20
				22 Feb–3 Mar 1982 (5)	237	6 May 1982	240	
				1–7 April 1982 (2)***		6 May 1982		
♂ 103330	48	alone	26 March 1980	19 April 1980 (1)	24**	23 June 1980		30
♀ 102671	15	with father and brother		26–29 Dec 1980 (6)	251	6 March 1981	250	32
				17–21 Aug 1981 (*)	231	28 Oct 1981	230	14
				20–24 Feb 1982 (*)	183	2 May 1982	186	
♂ 102668	26	alone	13 Feb 1981	6–11 March 1981 (4)	21**			
♀ 103561	7.5	with parents and two sisters		24–28 April 1981 (5)	44	6 July 1981		10
				24–27 Sept 1981 (*)	149	5 Dec 1981	152	2.5
				7–10 March 1982 (3)	161			
♂ 103462	11	with brother	13 April 1981	9–10 May 1981 (2)	26**			
♀ 103560	9.5	with sister		10 June 1981 (*)	31			
				5 July 1981 (1)	25			
				20 July 1981 (1)	15			
				13–14 Aug 1981 (2)	24			
				19–25 Sept 1981 (2)	36	30 Nov 1981		3.5
				5–9 April 1982 (3)	192	13 June 1982	195	
♂ 103461	11	with brother	13 April 1981	8 May 1981	25**			
♀ 103559	9.5	with sister						

* Copulatory tie not observed, but male mounting, female lordosis, and vulval swelling and redness seen.
** Pairing-to-estrus interval.
*** Copulation during pregnancy after pair moved to a new cage.

Males and females were introduced in one or two 30-min encounters from 0 to 18 days before being paired. After permanent cohabitation, pairs were observed for 3 to 3.5 h per week; family groups were observed 12 to 14 h per week. Comparative data on crab-eating foxes (*C. thous*) and maned wolves (*Chrysocyon brachyurus*) are from CRC records.

We defined estrus as the occurrence of (1) copulatory ties and/or (2) redness and swelling of the vulval region concurrent with the female's assumption of the lordosis posture and male mounting. An estrous period encompassed the days when we observed estrous behavior.

Captive bush dogs did not exhibit a fixed breeding season. The monthly breakdown of 28 recorded births was as follows: February, 2; March, 4; April, 1; May, 3; June, 3; July, 2; August, 2; September, 2; October, 1; November, 5; December, 3 (Dmoch, 1980–1981; Roben, 1974–1979; CRC records). Estrous periods were recorded in every month at CRC with an average of 3.6 ± 1.8 periods per month (range 1–6). Six litters of crab-eating foxes, also born at the CRC facility, were produced in the months of January, March, May, June, and October, suggesting aseasonality in this species as well (see also Brady, 1978). However, all 18 litters of maned wolves were born from December to February.

Estrous periods of bush dogs at CRC ranged from 1 to 12 days ($\bar{X}$ = 4.1 days; n = 22) (Table 1). Two young primiparous females (103560 and 103561) exhibited polyestrous cycling before they conceived, a condition never before reported for a canid. Interestrous intervals in these two females ranged from 15 to 44 days. Within a 1-year period female 103560 had seven estrous periods and gave birth to one litter, and female 103561 had four estrous periods and gave birth to two litters (see Table 1). The earliest age at conception was 10 months (female 103561).

Additional observations suggest that in bush dogs, estrus is suppressed in pubertal females when living alone, with sisters, or with one or both parents, and is stimulated once a female is paired with a male. Five primiparous females (age 7.5 to 17 months) which had shown no previous reproductive activity, exhibited estrous behavior within 4 weeks of pairing (range 5 to 26 days) (Table 1).

Two family groups, one with three female offspring and the other with three female and two male offspring, were kept intact for 7.5 and 10 months, respectively. In all instances, the juvenile females never exhibited physical or behavioral signs of puberty (they rarely or never urine marked unlike juvenile male littermates that regularly urine marked at 4 months of age; Porton, 1983) or reproductive activity while living with the parents. In one family, female 103561 (7.5 months) was removed from the group and came into estrus 22 days after being paired with a male. Nineteen days later, the two remaining sisters (103559, 103560) were separated from the parents and housed together. Although these females were visually monitored daily for signs of vulval swelling and redness, no changes were seen. A vaginal smear taken from female 103559 5 days after separation from the parents was characteristic of anestrus. Forty days after separation from the parents, the two sisters, now 9.5 months old, were paired with males, and copulated within 25 and 26 days respectively.

In another family group, the five 10-month-old siblings were separated from their parents and housed together, and within 11 days one of the females exhibited lordosis and accepted the mounts of a brother. In a third family, female 102671 remained housed with her father and brother for 16 weeks after her mother's death, when the female was 11 months old. No reproductive activity was detected in the trio. However, within 26 days of being paired with an unfamiliar male, the then 16-month-old female mated.

Typically, females have a 238 ±39.6 (range 179–301; n = 11) day interbirth interval (Dmoch, 1980–1981; Roben, 1974–1979; CRC records). Gestation averages 67 days (CRC records); thus estrus does not occur until approximately 171 days postpartum. However, the interval between a birth and the first subsequent estrus was significantly shorter in five females whose pups were removed before 4 months of age when compared with 11 females who raised young beyond 4 months (t = 6.15, $d.f.$ = 14, $P < 0.002$; Dmoch, 1980–1981; Roben, 1974–1979; CRC records). Three females at CRC, whose 2- to 4-month-old pups were removed for medical reasons not related to the quality of the females' parental care, came back into estrus 2, 5, and 21 days after the pups' removal (Table 1). Female 103561 had 2.5-week-old pups removed and bred 79 days postpartum. Similarly, pups from a female at the Frankfurt Zoo ("Frank 30"; Dmoch, 1980–1981) died at 4 days of age and, based on the subsequent birth date, the female mated approximately 80 days later. Thus, the interbirth interval may be shortened in females when their pups are removed or have died.

The above data indicate that bush dog reproduction in captivity is aseasonal and is influenced by social factors. Moreover, reproductive suppression of daughters probably occurs, a condition described primarily for mammalian species that are monogamous and live in family groups containing young of different ages, e.g., in marmosets and tamarins (Abbott and Hearn, 1978; Epple and Katz, 1980; Kleiman, 1979), in canids (Frame et al., 1979; Zimen, 1976), and in viverrids (Rood, 1980). In the wolf, *Canis lupus*, (Medjo and Mech, 1976) and in two callitrichid species (Abbott and Hearn, 1978; Epple and Katz, 1980), release from

parental influence results in reproduction at a younger age in pubertal females. We know little of bush dog social organization in the wild, but captive juveniles and parents continue to exhibit strong social bonds as long as they are housed together suggesting strong family bonds.

It appears that the reproductive strategy of the bush dog is one of essentially uninterrupted reproduction with the potential of a large number of young. However, the bush dog's lifetime reproductive potential is similar to other canids since bush dog litters are relatively small (average 3.8, range 1–6; $n = 32$ litters) (CRC records; Dmoch, 1980–1981; Emerson, 1972; Jantschke, 1973; Kitchener, 1971; Roben, 1974–1979), especially when compared to other group-living, pack-hunting canids. For example, wolf litters average four to 6.5 (range 1–9), African wild dog litters are usually seven (range 1–16) (Ewer, 1973), and dhole (*Cuon alpinus*) litters are typically eight (Johnsingh, 1979). Furthermore, teat numbers also vary interspecifically and in the same direction as litter size; wolves have 10 teats, African wild dogs 12 to 14, dholes up to 16, whereas bush dogs have 8 teats (Ewer, 1973). Thus, small litter size, small teat number, two estrous cycles per year, and reproductive flexibility appear to be coevolved traits in the bush dog.

All canids which have been reported to exhibit some degree of reproductive flexibility are tropical in distribution. However, not all tropical canids are reproductively flexible, e.g., the maned wolf. In addition to climate, seasonal variation in food availability most likely influences the reproductive timing of tropical species. Bush dogs probably prey on medium-sized mammals, such as agoutis (*Dasyprocta* spp.), paca (*Agouti paca*), capybaras (*Hydrochoerus hydrochoeris*), and small deer (*Mazama* spp.) (Deutsch, 1983; Langguth, 1975). Where they inhabit forest with permanent access to water, these prey species are typically stable in numbers and density (Collett, 1981; Macdonald, 1981; Smythe, 1978). A relatively stable prey base may have allowed year-round breeding by bush dogs and thereby permitted the timing of reproduction to be influenced by social factors.

There is an obvious need for more research on both the reproductive behavior and physiology of bush dogs and other tropical canids. At a time when the existence of many tropical species is threatened by habitat destruction, the need to understand their basic reproductive biology is even more urgent.

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