

A CASE OF INBREEDING IN THE AFRICAN WILD DOG *LYCAON PICTUS* IN THE KRUGER NATIONAL PARK

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Abstract – An observed case of inbreeding in a pack of wild dogs *Lycaon pictus* in the Kruger National Park, Republic of South Africa, provides evidence for the phenomenon of dominance reversal in this species. This is believed to be the first recorded instance of inbreeding in *Lycaon*. Emigration of subordinate females from established packs of wild dogs has been documented in the Serengeti National Park and Ngorongoro Conservation Area in northern Tanzania, as well as in the Kruger National Park. However, the newly subordinate (ex-dominant) female in the pack in which inbreeding has occurred has not emigrated in the 16 months since the change in her status. A possible explanation for this behaviour is given. As a result of this reversal, the pack contains at least two females capable of breeding, the subordinate of which is at least two years older than the dominant. This is considered the first record of such a breeding structure in *Lycaon*.

Introduction

Research over the past 15 years has shown that the wild dog is a social carnivore which preys primarily on the small to medium-sized ungulates of Africa (van Lawick 1970; Mitchell, Shenton & Uys 1965; Pienaar 1969).

Studies of cooperative pack hunting and non-aggressive relations at kills have led previous researchers to conclude that dominance is absent in *Lycaon* (Kuhme 1965; Estes and Goddard 1967; Schaller and Lowther 1969). More recently, however, van Lawick (1970) found that a domin-

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ance hierarchy is present within both sexes, but more clearly defined in females. Dominant individuals are recognized by their ritualized urine-marking of blades of grass (van Lawick 1970) or of such foreign objects as bones and hyaena *Crocuta crocuta* faeces (Reich 1977a). Breeding within the pack is restricted to the dominant pair, but both breeding and non-breeding individuals cooperate in the rearing of the young (van Lawick 1970).

Frame & Frame (1976) documented four positive cases of female group emigration and three possible cases of single female emigration in *Lycan* in the Serengeti National Park and Ngorongoro Conservation Area in northern Tanzania. In all seven cases, the emigrants were subordinate sisters or daughters of the dominant female. Such a system precludes the possibility of father-offspring inbreeding. However, the present study in the Kruger National Park (KNP), Republic of South Africa, first undertaken in June to August 1974 and resumed in October 1975, documents what is believed to be the first recorded instance of patrilineal inbreeding in *Lycan*.

Observations and Discussion

Inbreeding was observed in a pack which inhabits the southern section of the Park. Recorded changes in age and sex composition within the pack during the study are summarized in Table 1.

Table 1

Changes in age and sex composition of a pack of wild dogs in the Kruger National Park. October 1975–November 1977. Individuals up to the age of 12 months are pups. Juveniles are aged 12–24 months. Adults are 24 months and older. Shaded symbols indicate dominant male and female. Brackets indicate an individual whose sex is unknown. Vertical columns indicate the progress of an individual through an age class. Interruption of vertical column indicates death or disappearance of an individual. Arrows represent survivorship of pups to juvenile age class and recruitment of juveniles to adult age class.

Date	Adults	Juveniles	Pups
Oct 1975	♂♂♀♀♀♀(♂♀)		♂♀♀♀
Dec 1975	♂♂♀♀♀♀		♂♀♀♀
Jun 1976	♂♂♀	♂♀♀♀♀ ←	♂♂♀♀♀♀ (♂♀)
Jul 1976	♂♂♀	♂♂♀♀♀	♂♂♀♀♀♀ (♂♀)
Oct 1976	♂♂♀	♂♂♀♀♀	♂♂♀♀♀♀
Nov 1976	♂♂♀	♂♂♀♀♀	♂♂♀♀
Feb 1977	♂♂♀	♂♂♀	♂♀
Apr 1977	♂♂♀ ♀♂♀ ←	♂♀ ←	
Jun 1977	♂♂♀ ♀♂♀	♂♀	♂♀♀
Aug 1977	♂♂♀ ♀♂♀	♂♀	♂♀
Nov 1977	♂♂♀ ♀♂♀	♂♀	♂♀

In July 1976 one of the juvenile females, aged ± 15 months, was observed urine marking with the dominant male. This behaviour immediately identified the juvenile as dominant in the absence of her mother,

who remained at the dens with the 1976 litter. When the two females were seen together later that month, marking was performed solely by the juvenile female and dominant male. In April 1977, the new dominant female was pregnant. A litter was born in June of the same year.

For the past 16 months, the ex-dominant female has remained with the pack. She is clearly subordinate to her two adult daughters, one of which is the new dominant. In order to terminate bouts of female activity in which the ex-dominant plays with her non-breeding adult daughter (age \pm 30 months) and juvenile daughter (age \pm 18 months), the new dominant directs herself to the ex-dominant. Her posture is clearly dominant; ears are raised, and the tail is occasionally lifted. Although subordinate to her daughter, the ex-dominant's submissive gestures have always been active, employing the elements of a crouched stance, flattened ears and lowered tail (Schenkel 1967). Passive submission, in which belly, flank (Schenkel 1967) or neck (van Lawick 1970) is exposed, has been absent in this unique case, and may indicate a relatively high tolerance toward the non-breeding adult females on the part of the new dominant.

Recent reports have indicated that female emigration is the "regular and predictable pattern of interpack transference" amongst a population of wild dogs in the grasslands and woodlands of the Serengeti National Park and Ngorongoro Conservation Area in northern Tanzania (Frame & Frame 1976). Emigration in this population is a phenomenon restricted primarily to juveniles. However, secondary emigration exists, whereby sisters of a newly dominant emigrant leave the pack after she has attained this status. Furthermore, emigration of subordinates may take place amongst individuals up to the age of five years (Frame & Frame, *pers. com.*). The result of these emigrations, "in combination with probable mechanisms which delay some females' breeding" (Frame & Frame 1976) is a population consisting of a number of packs, each with only one breeding female.

The recent study in the KNP, however, has shown that a juvenile female may supplant a breeding female as dominant, assuming that status in the presence of the older individual. Since 1) females do not give birth before the age of two years; 2) virtually all individuals in the KNP are born in May-June; 3) the ex-dominant gave birth to a minimum of two litters; and 4) the ex-dominant has remained with the pack for the 16 months since the change in her status, she is, as of November 1977, at least 53 months of age, and probably 65 months or older. This would place her beyond the age at which the latest observed emigration has occurred. There are no indications, such as increasing distance from the active or resting pack, that her subordinate status will result in emigration.

As of May 1978, the status of the dominant and ex-dominant females remains unchanged. The ex-dominant is therefore at least 60 months of age, and probably 72 months or older. The lactating dominant was seen at her den on 22 May 1978 with four pups aged approximately one month.

In a study of the social dynamics of a captive pack of wolves *Canis lupus*, Zimen (1975) observed two subordinate females attack the dominant female, with the result that one of the two became the new dominant. Although no aggressive interactions had been observed in the *Lycan* pack before the switch in dominance, the observed changes in social status in the two packs are nevertheless similar. In both packs, two subordinate females moved up in the Rank Order at the expense of the dominant female, and in the *Lycan* pack the social activities of the ex-dominant were limited by the dominant behaviour of the new alpha female, while in the *C. lupus* pack, subordination was even more extreme, with both females and males occasionally attacking the ex-dominant, now termed "scapegoat" by Zimen. This scapegoat, along with the other subordinate female, gradually regained her "social freedom" (as termed by Zimen) before the mating season, a time in which Zimen describes the alpha female as "tolerant". Social activity of the two subordinates was later restricted by the dominant during the mating season. In *Lycan* society, similar changes in tolerance have been observed during the breeding season, especially with regard to access to denning pups. Reports from East Africa indicate that subordinate females are often prohibited from playing with the dominant females or, in extreme cases, their own pups (van Lawick 1974). These similarities suggest a close relationship between the two species, not only with respect to hunting behaviour (Mech 1975), but in social behaviour as well.

Size appears to be a primary factor in the determination of dominance in many vertebrate societies (Wilson 1975). But despite the fact that the ex-dominant in the inbreeding pack is smaller than her two adult daughters, it is doubtful that size plays an important role in *Lycan* society, since a number of packs are led by dominant individuals which are smaller than their subordinates. Although size cannot be excluded from the investigation of dominant-subordinate interactions in *Lycan*, hormone levels, health and nutrition are all probably of equal, if not greater, importance in the determination of dominance. Insofar as the dominant and subordinate positions changed while the ex-dominant remained at the dens with the new year's litter, a time in which she was frequently absent from kills and more dependent upon the other members of the pack for food, the latter two factors were probably of increased importance.

Why the ex-dominant has not emigrated is a question which requires further investigation. Frame & Frame (1976) suggest that emigration is precipitated by either visual or olfactory evidence of an all-male pack in an adjacent range. Since all-male packs have been absent from the study area surrounding the pack range for virtually the entire study period, the subordinates have had little opportunity to emigrate to a pack in which they would become dominant. The related aspects of natality, mortality, pack size and habitat predictability, and their interrelationship with the phenomenon of female emigration, is discussed elsewhere (Reich 1977 b).

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