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Social Organization of African Wild Dogs (*Lycaon pictus*) on the Serengeti Plains, Tanzania 1967—1978¹⁾

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With 8 figures

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Abstract

African wild dogs were studied from 1967 to 1978 on the Serengeti Plains in northern Tanzania. The main objectives were to determine the status of the sub-population and to elucidate the ecology and behavior of this social carnivore. This paper describes the decline of the sub-population, the dynamics of pack composition, and patterns of dispersal.

I. Introduction

As the results of long-term studies of the social organization of group-living mammals accumulate, it is becoming clear that in the majority of species the stable groups are composed of genetically related ♀♀. In these species, ♂♂ leave the group in which they were born, while a proportion of the ♀♀ remain permanently with their mothers and other female relatives (reviewed in WILSON 1975; EISENBERG 1977).

African wild dogs appeared to differ from the usual pattern of mammalian social organization by having stable groups of genetically related ♂♂, while all ♀♀ left their natal packs (FRAME and FRAME 1976). The purpose of the present paper is to further elucidate the social organization of this species; the 4 authors combine their data to provide 10½ yrs of continuous records of wild dog packs.

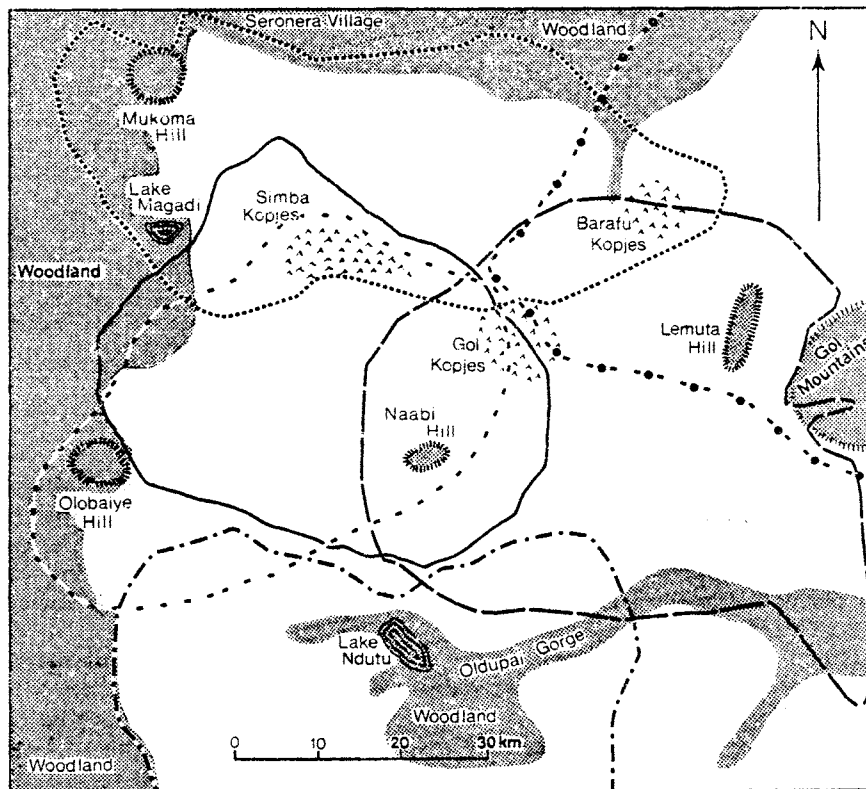
The African wild dog is a pack-hunting carnivore that ranges over much of sub-Saharan Africa outside the equatorial lowland-forest zone (DORST and DANDELOT 1970). Wild dogs in East Africa stand 75 cm tall at the shoulder and weigh 20—25 kg. There is no sexual dimorphism in size. Maximum life span recorded was 11 yrs (this study). Previous work on the species was summarized by SCHALLER (1972), and hunting behavior was described by ESTES and GODDARD (1967) and MALCOLM and VAN LAWICK (1975). Packs have only

¹⁾ This is S.R.I. Contribution No. 218.

one dominant breeding pair, and all adult members of a pack help to raise pups (MALCOLM in prep.). The adults regurgitate meat to the pups from the age of 3—12 wks, and then the pups leave the natal den and follow the pack as it hunts (VAN LAWICK 1970). At 9—11 mo old, pups begin killing easy prey, but they are not proficient hunters until they are 12—14 mo of age (ms. in prep.). The communicatory gestures of African wild dogs are similar to those reported by SCHENKEL (1947) and FOX (1971) for other canids.

II. Study Area

We observed wild dogs from April 1967 through January 1978 on the Serengeti Plains in the Serengeti National Park and Ngorongoro Conservation Area in northern Tanzania. From 1967 to 1972, we searched an area of 3000 km² centered on Naabi Hill (Figs. 1, 6). From 1973 to 1978 the search area was expanded to 5200 km², which included 4200 km² of short and medium grasslands and 1000 km² of the surrounding *Acacia* woodlands. This study area was selected because the open vegetation and even terrain were conducive to sighting



- | | |
|------------------------------------|--------------------------------------|
| Seronera Pack (50 sightings) | ----- Genghis Pack (36 sightings) |
| ———— Plains Pack (49 sightings) | - - - - Spitfire Pack (14 sightings) |
| - - - - Kühme Pack (37 sightings) | •••• Semetu Pack (6 sightings) |

Fig. 1: Study area of wild dogs on the Serengeti Plains, Tanzania. The known extent of home ranges of 6 packs is shown. Boundaries were approximated by drawing a polygon around all locations where each pack was seen from August 1973 through January 1978. Each home range was about 1500—2000 km², but these boundaries include shifts that occurred during the 4½-yr period

and following wild dogs. For an ecological description of the area see NORTON-GRIFFITHS and SINCLAIR (1979).

The Serengeti Plains undergo dramatic seasonal fluctuations of migratory prey. In the wet months (Nov.—May) more than 1 million wildebeests (*Connochaetes taurinus*) together with large herds of zebras (*Equus burchelli*), elands (*Taurotragus oryx*), and Thomson's gazelles (*Gazella thomsoni*) graze the plains. In the dry season the area supports small resident herds of Grant's gazelles (*G. granti*) and Thomson's gazelles. Spotted hyenas (*Crocuta crocuta*), lions (*Panthera leo*), golden jackals (*Canis aureus*) and black-backed jackals (*Canis mesomelas*) are present year round.

III. Methods

H. VAN LAWICK did his fieldwork in 1967 and 1968—1969; H. VAN LAWICK with J. MALCOLM in 1970, 1971, and 1972; J. MALCOLM in 1976—1977; and L. and G. FRAME from 1973—1978.

Most packs were found by scanning large areas with binoculars, often from high places in the early morning and late afternoon when wild dogs are usually active. Occasionally we used radio telemetry and visual searching from light aircraft. Wild dog locations were often reported to us by other scientists and visitors. The low population density (as little as 1 dog/200 km²) and the large home range of each pack made it impossible to locate packs at will. A pack was usually found after 1—10 days of searching.

Age and sex composition were recorded for all sightings. "Pups" were less than 1 yr old, and were clearly distinguishable by their smaller size. All dogs over 1 yr of age were termed "adults". Exact ages of most adults were known from our records.

Packs were followed in a 4-wheel-drive vehicle. Wild dogs are tolerant of cars, and were observed from 10—30 m unless they were traveling or hunting. At night, resting dogs were watched by moonlight or low-intensity lights. Observations on moving dogs varied from 1—9 consecutive days; longer periods of observation were possible at natal dens.

Most wild dogs were photographed when first seen. Each dog has a unique coat pattern of white and yellow markings on a brownish-black background. The white markings are present at birth (DEKKER 1968). The yellow splotches develop from the dark area and are first visible at 4—5 wks, but become more intense through the first 5 mo. Photographic comparisons show that coat markings do not change with age after the first 5 mo. When relocated, dogs were identified from the photographs, and this provided information on the changes in group composition.

Certain dogs within packs had very similar coat markings. This was quantified (by J. R. MALCOLM) by enlarging the photographs to quarter-plate size (10.4 × 8 cm) and overlaying a piece of clear plastic scored with a 2.5 mm grid. The number of squares overlying white spots was counted and calculated as a proportion of the total surface area of that dog. The area analyzed excluded the tail, head, and neck, which showed more or less invariable coat markings. In cases where both sides of a single dog were analyzed, the final score used was the mean of the two sides. Photographs were analyzed in a randomized sequence, and recalculations of the same photographs gave a mean error of 6.5%. The scores from the population showed a highly skewed distribution, and were transformed by taking log₁₀ of each score before computing a one-way analysis of variance for 36 dogs from 5 litters. There was significantly less variance in white spotting within than between litters ($F = 6.8$; $p < .001$). The yellow markings on related individuals also seem less variable than between unrelated dogs, but no reliable method was found to demarcate areas of yellow where they graded into dark areas. The results suggest that dogs within a pack with similar amounts of white and yellow are often littermates.

Observations on the behavior of dogs were entered on checksheets or dictated into tape recorders and later transcribed. Focal animal sampling was found to be useful in some situations. Most behavior observations were made using binoculars.

IV. Results

A. The Sub-population

During 1967—1972 12 packs were identified. Most information in this period came from a single large group, the Genghis Pack, whose range occupied the center of the study area (cf. VAN LAWICK 1970, 1973). In 1973,

monitoring of 4 packs was begun, and from January 1975 until the end of the study, detailed records on 6 packs were maintained. Four of these 6 packs had been observed prior to 1970.

No new wild dogs were found between September 1970 and October 1973. All adults seen in that period were known either from photographs taken earlier, or as pups born after the study began. The study area was expanded after October 1973. In the subsequent year 2 more packs were discovered, and 3 dogs of unknown ancestry joined existing packs in the study area. Thereafter, until the end of the study, no strange adult dogs were seen in any study packs. However, in February 1977, a completely new pack of 3 adults (2 ♂♂ and 1 ♀) appeared and became resident in the central part of the study area. Probably all individuals resident in the study area were identified for the years 1970—1977.

Table 1: Wild dog numbers and group sizes on the Serengeti Plains, Tanzania

	1970	1974	1975	1976	1977
Total number of identified adults seen alive in the study area	95	49	62	29	26
Number of packs*	12	7	8	5	7
Mean adult group size**	6.5	6.3	6.9	4.7	3.6
Mean number of adult ♂♂ per group***	4.1	4.1	4.5	3.1	2.5
Mean number of adult ♀♀ per group***	2.6	2.2	2.4	1.7	1.2

* Groups containing a breeding pair.

** from 130 calendar-quarter groupings that include packs, lone dogs, and all other associations.

*** from 114 calendar-quarter groupings in which the sex of every individual was known.

The wild dog sub-population declined during the study. In 1970, the number of adults was 95. By 1974 the number had fallen to 49. The decline may have permitted the immigration of the new pack of 3 dogs in 1977; however, even with this addition, the sub-population was reduced to 26 adults in that year (Table 1). These figures represent densities of 1 adult/35 km² in 1970, and 1/200 km² in 1977 in the enlarged study area. Between July 1974 and January 1976 no pups survived to 1 yr old. Food competition with spotted hyenas (ms. in prep.) and disease caused most pup mortality.

B. Movements

Each pack ranged over an area of about 1500—2000 km², and shared parts of its range with each of its 3 or 4 neighboring packs (Fig. 1) (ms. in prep.). We never recognized deliberate avoidance of contact between packs. When packs met, one chased the other from the vicinity; usually the smaller pack fled from the larger. Pack movements were most clearly correlated with hunting success. When prey were scarce, packs commonly traversed the full width of their range in 2 or 3 days. Movements were more restricted when the dogs were at a natal den with young pups.

C. Sex ratio

There were more ♂♂ than ♀♀ in the sub-population. Of 151 different adult wild dogs sexed, 97 (64%) were ♂♂ (normal approximation, $Z = 7.1$, $p < .001$). The sex ratio at birth could not be determined because pups did not appear outside their natal dens until they were about 3½ weeks old. However, of 96 pups sexed in their first month of life, 57 (59%) were ♂♂ (normal

approximation, $Z = 3.6$, $p = .0011$) (MALCOLM in prep.). The bias toward $\delta\delta$ is most pronounced in older adults. Of 24 adults more than 5 yrs old, 18 (75%) were $\delta\delta$. A preponderance of $\delta\delta$ has been reported by other authors (ESTES and GODDARD 1967; SCHALLER 1972; PIENAAR 1969; STEVENSON-HAMILTON 1947). However, DELEYN (1962) reported a sex ratio skewed toward ♀♀ .

D. Groupings

We defined *pack* as a real or potential breeding unit composed of at least 1 unrelated adult δ and ♀ , or at least one adult with dependent pups. The term *group* was used for any association between individuals at a particular time, and included packs and lone dogs.

We tried to identify the group size in which a wild dog lived most of its life. To do this, all sightings were categorized according to the calendar quarters in which they occurred. All individual dogs were then assigned to the group in which they spent the most time in each 3-mo period. Results were as follows:

In a sample of 130 quarterly groupings, the mean group size (adults plus pups) was 9.8 (range 1–26). Mean adult group size was 6.0 (range 1–18). Pups were present in 45% of the groups. The mean number of pups, where they were present, was 8.8 (range 1–16). The proportion of pups in the population was 0.39 for the entire study period. Lone dogs were seen during 3 calendar quarters, accounting for 2.3% of all groupings.

All dogs were sexed in a sample of 114 quarterly groupings. The mean number of adult ♀♀ was 2.1 (range 0–7). A single ♀ was present in 52% of the groups. The mean number of adult $\delta\delta$ was 4.1 (range 0–10). Breeding units comprised 92% of the groups. Mean number of adult $\delta\delta$ and ♀♀ per group are represented annually in Table 1.

The decline in the number of wild dogs in the study area resulted in fewer breeding units as well as reduced mean group size. The number of packs fell from 12 to 7 between 1970–1974, and then remained almost constant. However, mean group size was maintained around 6.5 through 1975, and then declined significantly ($\text{LSD} = 1.515$, $p < .05$) in the following year where it remained with no significant change through 1977 (Table 1).

To compare our results with those of others, we used 254 sightings of wild dogs that we recorded from 1967–1978. All groups sighted were included. Groups seen more than once on a single day, or followed continuously, or resident at a den were counted as one sighting. Results were as follows: Mean total group size was 8.9. The mean adult group size was 5.9. These results were similar to those reported by others in the Serengeti; KRUUK and TURNER (1967) found a mean group size of 9.2, and SCHALLER (1972) reported a mean group size of 9.8 for the period 1967–1971 (his figures excluded pups less than 3 mo old). From other parts of Africa, PIENAAR (1969) reported mean group size in the Kruger National Park, South Africa, as varying from 8–11. DELEYN (1962) recorded a mean group size of 11 from Akagera Park, Rwanda.

The results of the calendar-quarter grouping method and the independent-sightings method are similar: 9.8 vs. 8.9 mean total group size, and 6.0 vs. 5.9 mean adult group size.

E. Dominance relations

A wild dog pack is a discrete and cohesive social unit that travels, hunts, and rests together. Amicable relations and food sharing have been emphasized

by other observers (e.g. KÜHME 1965; ESTES and GODDARD 1967), but even while the pack feeds together the breeding pair has priority over the preferred parts of food (ms. in prep.). Dominant dogs were not always leaders in hunting.

Ritualized displays of dominance and subordination seen in other canids, such as wolves (SCHENKEL 1947), can be identified in *Lycaon*, and when quantified reveal separate linear hierarchies among the adult ♂♂ and adult ♀♀ in a pack. Adult patterns of agonistic behavior are evident by 1 yr of age; at this time hierarchies are most clearly expressed between members of the same sex from the same litter (ms. in prep.).

Only the alpha ♂ and the alpha ♀ (i.e. the breeding pair) in a pack regularly urine-marked, often simultaneously on the same place, with one or both hind legs raised (VAN LAWICK 1970). The dominant pair in most packs had higher-than-average frequencies of interaction (ms. in prep.). They threatened and fought their same-sex relatives who tried to breed, and usually succeeded in monopolizing reproduction. The dominant pair generally determined movements of the pack within its range, either by direct leadership or by refusing to follow subordinate dogs (ms. in prep.).

No alpha ♀ lost her status. The tenure of alpha ♀♀ ranged from 1—8 yrs. Fights that led to a change of status among subordinate ♀♀ were seen twice.

The breeding ♂ and his brothers dominated older and younger ♂♂ in their pack. On 3 occasions, a breeding ♂ defeated challengers, but in 7 cases the breeding ♂ lost his status to younger relatives in transitions we did not witness. In addition, in 2 packs more than one ♂ from a litter was dominant at different times. The tenure of breeding ♂♂ ranged from 1—7 yrs.

F. Reproduction

Full mating behavior culminating in a brief copulatory tie (up to 6 min duration) was seen in 5 packs. In 4 cases mating was restricted to the dominant pair. In the other pack, the dominant ♀ mated with 3 ♂♂ (VAN LAWICK 1973).

The age of first mating for 5 ♂♂ was verified as 1³/₄, 2³/₄, 3, 3, and 5 yrs. The oldest known ♂ to mate was 7¹/₂ yrs old.

The youngest ♀ known to give birth was about 22 mo old at whelping. Of 5 ♀♀, 3 first whelped when less than 3 yrs old, and the other 2 when 3¹/₄ yrs old. The oldest ♀ to have a litter of pups was 8 yrs old.

The birth interval for adult ♀♀ was 12—14 mo when some pups survived. When the litter perished, the interval was as short as 6 mo.

Pups were born in every month of the year, except September. An analysis of 31 litters born during this study, plus 14 other litters reported by SCHALLER (1972) showed a peak of births in April, with 60% of all known litters born from March through June. Thus most litters were born during the period defined by NORTON-GRIFFITHS, HERLOCKER and PENNYCUICK (1975) as the second half of the rainy season. Mean litter size, calculated from 15 litters counted when the pups first appeared, was 10.1 (range 6—16). This excluded litters in which mortality was known to have occurred.

Normally only the alpha ♀ in a pack produced pups. Sexually mature daughters (i.e. more than 1¹/₂ yrs old) were never known to breed while in their natal packs. After transferring to another pack, however, sisters of the dominant ♀ sometimes bred. Only 4 of 16 subordinate sisters tried to rear litters, but at least 2 of these ♀♀ attempted more than once.

We recorded 6 litters born to subordinate ♀♀ during a period when the dominant ♀♀ of the same packs whelped 9 litters. KÜHME (1965) also recorded

a subordinate ♀ whelping. In 5 of the 6 litters the subordinate ♀ had her litter at the same time as the dominant ♀, and after the pups reached 4—5 wks old, competition between the mothers was severe. The dominant ♀ apparently wanted to control all access to the pups, and interfered with their provisioning. The only instance in which a subordinate ♀ was known to raise pups occurred in a pack where the dominant ♀ did not give birth at the same time; this pack was large, with 12 adults, and was killing very large prey, such as zebras, at the time.

G. Pack dynamics

Pack composition and the movement of dogs between packs are summarized in Figs. 2—5. On each Fig., the vertical axis represents time, and each dog occupies one column unless it moved to another pack, as indicated by a diagonal line. The pack composition is reentered in the figure each time it differed from the last sighting.

Most wild dog groups consisted of several related adult ♂♂ (often from more than one generation), one or more fully adult ♀♀ (sisters who were unrelated to the adult ♂♂), and pups or young adults who were born into the pack. Only about 15% of the quarterly groupings did not conform to the typical pattern; these included groups of same-sex adults, heterosexual pairs

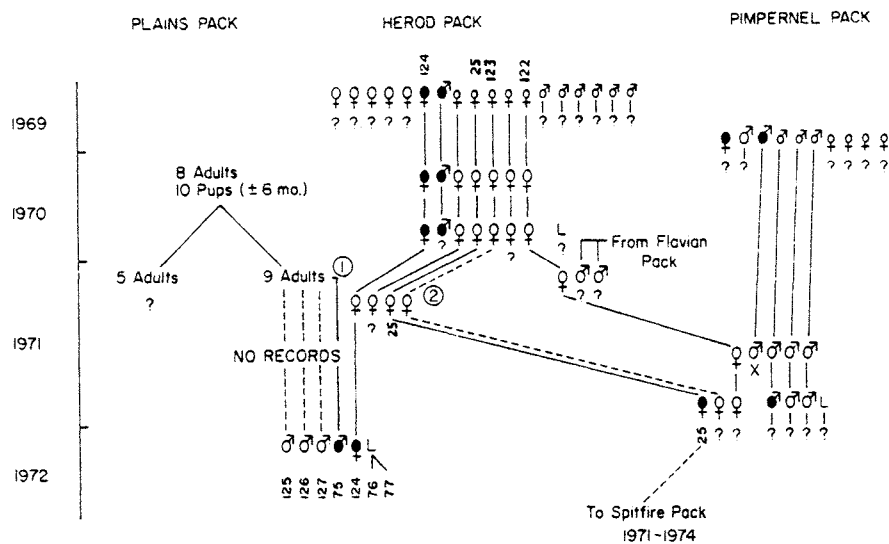


Fig. 2: Changes in the composition of wild dog packs on the Serengeti Plains, Tanzania — Plains, Herod, and Pimpernel Packs, 1969—1972. Each dog occupies a single vertical column through time, and movement in or out of the pack is indicated by a diagonal line. Numbered columns identify individuals mentioned elsewhere. Key: ● Dominant breeding adult; ♂♀ adult (over 1 yr old); ○ sex unknown; ♂♀ pup (less than 1 yr old); L whole litter; × probably died; ? disappeared. 1. A pack of 9 adults was located in January 1971. At least 5 individuals had been seen in the Plains pack in 1970. 3 of the 4 ♂♂ in the Plains pack in 1972 had been in the Plains pack in 1970. One ♂ had been identified in 1970, 1971 and 1972. 2. A pack of 13 adults was sighted in February 1971. At least 4 dogs came from the Plains pack. The old ♀ and 2 young ♀♀ from the Herod pack were also identified. From the size of the pack, we think that it is likely that a third young ♀ from the Herod pack was also in the pack. The third ♀ had certainly joined the Pimpernel pack by May 1971, together with two of her littermates

which sometimes whelped, and one group (Fig. 2, the Herod Pack) where a pair of adults whelped in the absence of male kin but in the presence of 5 2-yr-old female littermates that had been born in the pack.

Wild dog groups changed in adult composition, other than by deaths, in the following 4 ways: (1) Recruitment into the parent pack of juveniles born into that group, (2) primary emigration, the dispersal of young from the parent pack with transfer to another group, (3) secondary emigration, the dispersal of older subordinates, usually siblings of the dominant breeder, from the pack with transfer to another group, and (4) pack fission, in which 2 new breeding units, i.e. packs, are formed from one larger group.

1. Recruitment into the parent pack

Some wild dogs remained in the packs where they were born. All documented cases of offspring dispersal involved dogs that were less than 3 yrs old. Any dog that was still in its natal pack at the age of 3 yrs, therefore, was classified as having been recruited.

No ♀ born during the study was known to remain in her natal pack. In one case, the single surviving ♀ from a litter was still in her parent pack at the age of 2½ yrs, but neither she nor her parent pack was seen again.

Recruitment of ♂♂ was relatively common. There were 38 ♂♂ born during the study who survived to be 1 yr old, and whose parent packs were still under observation when the sons were past 3 yrs old. Of these 38 ♂♂, 17 (45%) were recruited, 6 ♂♂ almost certainly emigrated (Table 2), and the remaining 15 ♂♂ (Table 3) probably experienced some mortality while they were still members of the parent packs. So 55% is an overestimate of the total proportion of ♂♂ that emigrated.

Other circumstantial evidence indicated that ♂ recruitment was common. Adult ♂♂ older than the breeding ♂ were present in 57% of the 92 calendar-quarter groupings in which all dogs' ages were known. As no unrelated ♂ was ever known to join a pack, these older ♂♂ probably constituted the remnants of the parent pack in each case, and the dominant ♂ and his brothers had been recruited.

Packs were named on the basis of their continuing male kin lines. In 2 cases male kin lines persisted for 10 yrs or more.

The most extensive male kin line record comes from the Genghis Pack (cf. Fig. 3). In April 1967, the Genghis Pack contained 1 adult ♀, 4 adult ♂♂, and 6 large male pups that were born in the pack in 1966 (3 of which were ♂42, ♂130, ♂131). Between April 1967 and February 1971, the 4 very old ♂♂ disappeared singly; because no other pack members disappeared with them, we assumed that they had died. The 6 young ♂♂ were recruited. In July 1969, another litter was born containing 3 ♂♂; 2 of these (♂43, ♂44) were permanently recruited into the pack and 1 disappeared. In 1971, another litter was born, but not all the pups were cataloged. In the following year an adult ♂ was seen in the pack who had coat markings similar to other pups born to the breeding ♀, so we assumed he was born in the pack. Between 1973 and December 1975, the 6 ♂♂ born in 1966 all died. Of 3 male pups from the 1974 litter who survived to be 1 yr old, only ♂49 was still in the pack in late 1975. By 1977 the pack contained the 2 ♂♂ recruited from the 1969 litter, the ♂ recruited from the 1974 litter, and 1 female immigrant.

The other well-known male kin line is the Kühme Pack. One of the ♂♂ photographed by W. KÜHME in 1964 was still alive in 1968, but was not seen

thereafter. Another ($\delta 60$) remained in the pack until the end of 1976, at which time he was 11 yrs old (Fig. 4). All surviving $\delta \delta$ from litters born in 1968, 1969, and 1973 were recruited into their natal pack. By 1977, however, the only survivor of this kin line was the single male recruit of the 1973 litter ($\delta 62$) (cf. Fig. 5).

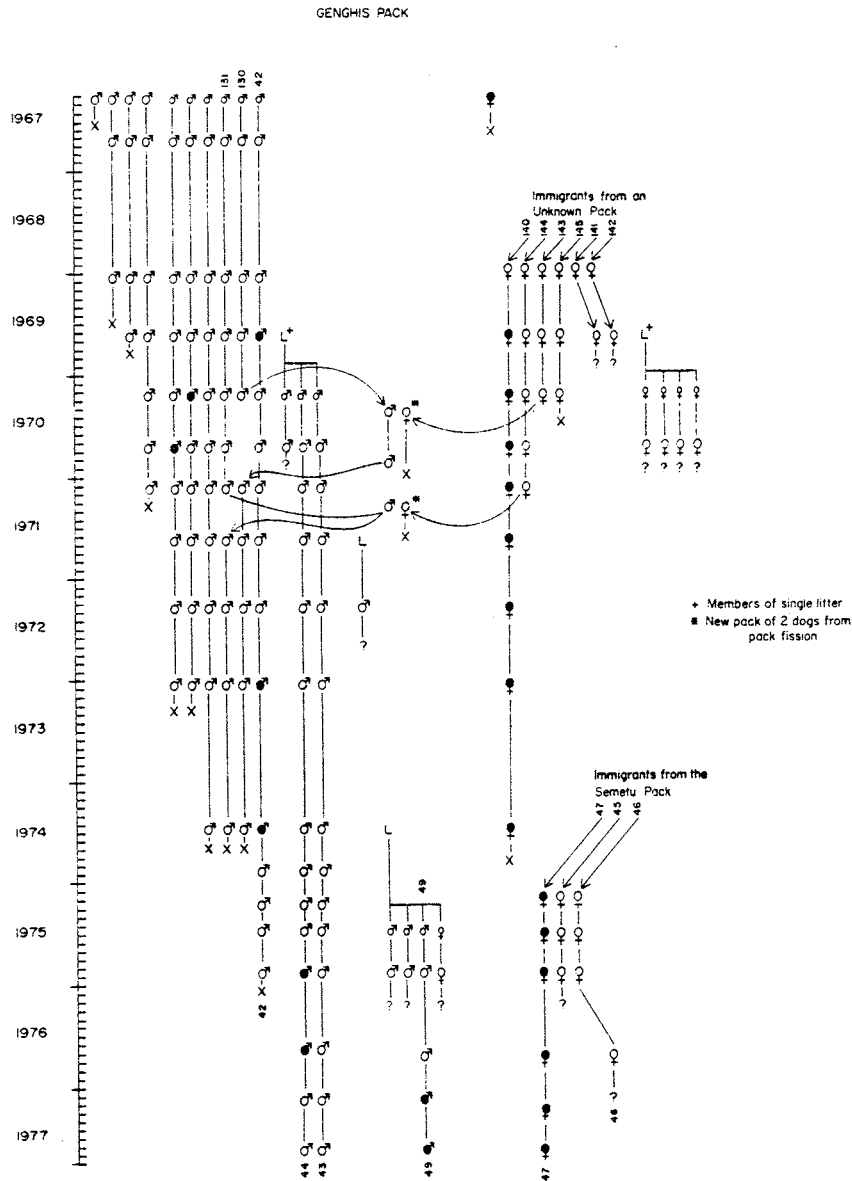


Fig. 3: Changes in the composition of wild dog packs on the Serengeti Plains, Tanzania — the Genghis Pack, 1967—1977. Each dog occupies a single vertical column through time, and movement in or out of the pack is indicated by a diagonal line. Numbered columns identify individuals mentioned elsewhere. Key: ● Dominant breeding adult; $\delta \delta$ adult (over 1 yr old); \circ sex unknown; \circ pup (less than 1 yr old); L whole litter; X probably died; ? disappeared

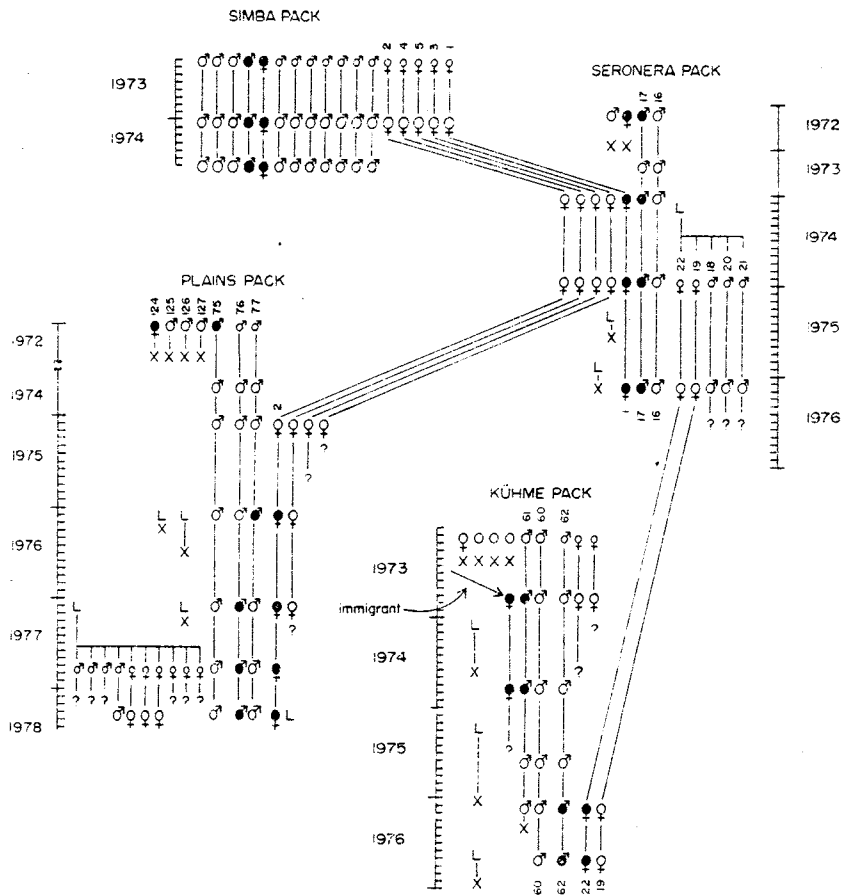


Fig. 4: Changes in the composition of wild dog packs on the Serengeti Plains, Tanzania — Simba, Seronera, Plains, and Kühme Packs, 1972—1978. Each dog occupies a single vertical column through time, and movement in or out of the pack is indicated by a diagonal line. Numbered columns identify individuals mentioned elsewhere. Key: ● Dominant breeding adult; ♂ ♀ adult (over 1 yr old); ○ sex unknown; ♂ ♀ pup (less than 1 yr old); L whole litter; X probably died; ? disappeared

The 17 ♂♂ known to have been recruited into their parent packs were from 7 litters. At least 1 ♂ from each litter (8 ♂♂ in all) bred in his natal pack. No ♂ bred with his own mother.

2. Primary emigration

Wild dogs commonly left their natal packs in which there was a dominant breeder of the same sex (usually the parent). This was termed *primary emigration*. Group emigration of littermates was common. But only siblings of the same sex were known to emigrate together (Figs. 2—5).

57 dogs between the ages of 1—3 yrs old left their natal packs. Of these, 19 were verified primary emigrants (including two probable cases involving 3 ♂♂ each) (Table 2); some of the remainder probably died while still members of the natal pack. All verified primary emigrations occurred in January, February, and March, when prey were abundant.

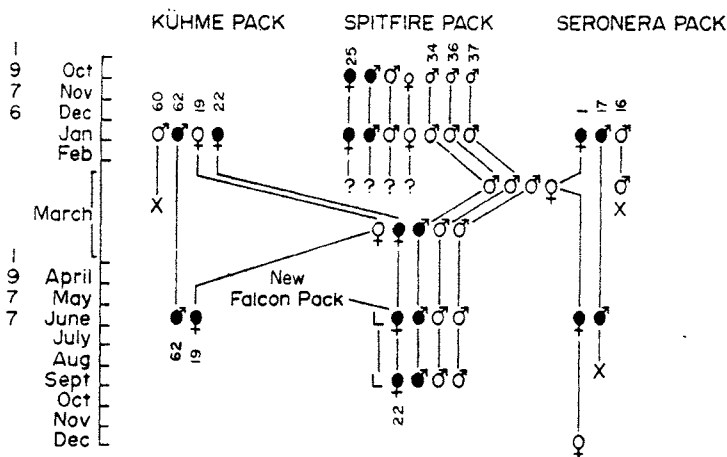


Fig. 5: Changes in the composition of wild dog packs on the Serengeti Plains, Tanzania — Kühme, Spitfire, Seronera, and Falcon Packs, 1976—1977. Each dog occupies a single vertical column through time, and movement in or out of the pack is indicated by a diagonal line. Numbered columns identify individuals mentioned elsewhere. Key: ●♀ Dominant breeding adult; ♂♀ adult (over 1 yr old); ○ sex unknown; ♂♀ pup (less than 1 yr old); L whole litter; × probably died; ? disappeared

A successful transfer involved the emigrants joining a different group that contained a dominant breeder of the opposite sex. In all verified transfers, at least 1 member of each emigrant group mated within a few months. The mean age for first breeding for 5 known-age emigrants (♂ and ♀♀) was less than 2½ yrs.

Table 2: Primary emigrations of wild dogs on the Serengeti Plains, Tanzania, 1969—1978. Primary emigration was the departure of young adults (1—3 yrs old) from the pack in which they were born. Their parents or some other older-generation relatives were the dominant breeders of their parent pack

♀♀	
<u>Verified Emigrations:</u>	<u>Disappearances:</u>
3 daughters (♀ 25, ♀ 122, ♀ 123) from Herod Pack joined Pimpernel Pack, 1971	1 daughter from Herod Pack, 1970
5 daughters (♀ 1, ♀ 2, ♀ 3, ♀ 4, ♀ 5) from Simba Pack joined Seronera Pack, 1974	1 Herod Pack daughter from her mother's new pack, 1971 (cf. Fig. 2)
3 daughters (♀ 45, ♀ 46, ♀ 47) from Semetu Pack joined Genghis Pack, 1975	1 daughter from Kühme Pack, June 1975
2 daughters (♀ 19, ♀ 22) from Seronera Pack joined Kühme Pack, 1976	1 daughter from Kühme Pack, July 1975
	1 daughter from Spitfire Pack, 1976
<hr/> 4 cases (13 ♀♀ total)	<hr/> 5 cases (5 ♀♀ total)
♂♂	
<u>Probable Emigrations:</u>	<u>Disappearances:</u>
3 sons (♂ 34, ♂ 36, ♂ 37) from Spitfire Pack formed the new Falcon Pack, 1977	
3 sons (♂ 18, ♂ 20, ♂ 21) left Seronera Pack together; their 2 sisters emigrated a month earlier, 1976	
<hr/> 2 cases (6 ♂♂ total)	<hr/> 0 cases (0 ♂♂ total)

There were 4 verified instances of primary emigration of groups of ♀♀ (Table 2). In each case the composition of the pack which the ♀♀ left, as well as the composition of the pack which they joined, was known.

Less direct evidence for primary emigration by ♀♀ came from 9 other packs in our study (Tables 2 and 3), where groups of sisters 1–3 yrs old disappeared from their mothers' packs. SCHALLER (1972) also reported an example where 3 sisters left their parent pack, while their 5 brothers stayed with the parents and helped raise pups.

Table 3: Unexplained disappearances of wild dogs less than 2 yrs old on the Serengeti Plains, Tanzania, 1969–1978. The time period between sightings was too long to determine how the dogs were grouped when they left the pack. Young adults 12–18 mo old are more susceptible to disease than are older adults, so disappearances may be the result either of death while in the natal pack or of emigration

5 adult ♀♀ c. 2 yrs old (possibly sisters or daughters of the dominant ♀) disappeared within 6 mo of another litter of 6 young adult brothers c. 1 yr old (sons of the dominant breeding pair) from the Herod Pack, 1969.
4 young adult sisters and 1 brother 12–18 mo old disappeared from the Genghis Pack, 1970.
3 young adult sisters and 4 brothers 12 mo old disappeared from the Spitfire Pack, 1975.
3 young adult sisters and 1 brother 12–18 mo old disappeared from the Pimpernel Pack, 1970.
3 young adult sisters and 3 brothers 13–14 mo old disappeared from the Plains Pack, 1978.

Another probable case of female primary emigration was the appearance of 6 new ♀♀ in the Genghis Pack in December 1968 (Fig. 3). These ♀♀ were young, appeared to be the same age, and had coat markings very similar to each other, but strikingly different from the adult ♂♂ in the pack. The ♀♀ were not members of the litters born in 1966 or 1967, and therefore must have come from another pack (Table 6).

There were 2 probable cases of primary emigration of ♂♂ (Table 2). One involved a group of 3 brothers who, at 2½ yrs old, left their parent Spitfire Pack and acquired a breeding ♀ by violence. This could not be classified as verified emigration by our criteria, because their parent Spitfire Pack was never seen again. But the movement of the ♂♂ out of their natal pack's home range was clearly documented. The second example was of 3 young ♂♂ who disappeared together from their parent pack soon after their sisters emigrated.

Possible cases of primary emigration by ♂♂ came from 5 more packs in which young adult ♂♂ disappeared (Table 3).

Emigrating ♂♂ traveled far into the ranges of adjacent packs, and beyond. Only 3 (14%) of the 21 young adult ♂♂ that disappeared from their parent packs were ever seen again. In contrast, 13 (36%) of 36 young ♀♀ were seen again as immigrants to other groups within the study area. This may reflect the lack of breeding opportunities for emigrant ♂♂ within the study area.

3. Secondary emigration

The dispersal of subordinate wild dogs from a pack where one of their siblings was dominant was termed *secondary emigration*. Although the average pack contained 2 adult ♀♀, subordinate adult ♀♀ never remained permanently in a pack with a dominant sister. Eventually every stable breeding unit was reduced to 1 ♀ (the dominant), plus 2 or more ♂♂ (Figs. 2–5). As in primary

emigration, siblings of the same sex emigrated together. But it was also common for lone individuals to undergo secondary emigration.

There were 3 verified cases of secondary emigration of 7 ♀♀ (Table 4), which occurred in November through May, the rainy season. In each case the composition of the pack which the ♀♀ left and the composition of the pack they joined were known.

Less certain examples of secondary emigration occurred 5 other times (Table 4).

Table 4: Secondary emigrations of wild dogs on the Serengeti Plains, Tanzania, 1969—1978. Secondary emigration was the departure of subordinate siblings (2—5 yrs old) from their dominant sibling's pack. This occurred following primary emigration of the sib-group, and assumption of breeding dominance by one of its members

♀♀	
<u>Verified Emigrations:</u> 2 sisters (♀141, ♀142) of Genghis Pack's breeding ♀ left together, late 1968 4 sisters (♀2, ♀3, ♀4, ♀5) of Seronera Pack's breeding ♀ left and roamed 3½ mo before joining Plains Pack, 1975 1 sister (♀19) of Falcon Pack's breeding ♀ left her and returned to the dominant ♂ of Kühme Pack, 1977 <hr/> 3 cases (7 ♀♀ total)	<u>Disappearances:</u> 1 sister (♀145) of Genghis Pack's breeding ♀, 1970 1 sister (♀3) of Plains Pack's breeding ♀, July 1975 1 sister (♀5) of Plains Pack's breeding ♀, July 1975 1 sister (♀4) of Plains Pack's breeding ♀, May 1977 <hr/> 4 cases (4 ♀♀ total)
♂♂	
<u>Verified Emigrations:</u> <hr/> 0 cases (0 ♂♂ total)	<u>Disappearances:</u> 1 brother of Genghis Pack's breeding ♂, 1972 <hr/> 1 case (1 ♂ total)

No ♂♂ were verified emigrants from their brother's pack, except in cases of pack fission. In some cases old ♂♂ disappeared singly from packs, but if they were 8 yrs or older we assumed they had died.

4. Pack fission

Sometimes groups consisting of at least 1 ♂ and 1 ♀ (unrelated to each other) emigrated together in what we called *pack fission* — the phenomenon in which a pack divided to form 2 separate breeding units. In such cases subordinate ♀♀ left their sister's pack, possibly at the time they were in estrus, and were accompanied by one or more subordinate ♂♂.

Pack fission was seen 3 times, and may have occurred on one other occasion (Table 5). In 2 of the verified instances of pack fission, the single ♂♂ involved eventually returned to their brothers' pack without their mates (Fig. 3). In the third verified case, ♂♂ of 2 generations (2 of which were ♂16 and ♂17) from the Cassidy Pack split away from the dominant ♂'s pack, accompanied by one unrelated adult ♀.

A probable case of pack fission also was recorded by ESTES and GODDARD (1967) in the nearby Ngorongoro Crater, when 8 dogs from a pack of 21 were seen hunting together through a period of 1 yr; the rest of the pack was not seen again.

Table 5: Fission in packs of wild dogs on the Serengeti Plains, Tanzania, 1969—1978. Fission was the departure of unrelated ♂♂ and ♀♀ together, which resulted in a new breeding unit

1 sister (♀ 143) of dominant ♀ and 1 brother (♂ 130) of dominant ♂ left the Genghis Pack together in 1970; the ♂ later returned without the ♀.
1 sister (♀ 144) of dominant ♀ and 1 brother (♂ 131) of dominant ♂ left the Genghis Pack together in 1971; the ♂ later returned without the ♀.
1 sister of dominant ♀ and 3 related ♂♂ (♂ 17 and his brother, and the older ♂ 16 who may have been the brother of the dominant ♂ of the original pack) left the Cassidy Pack together in 1971. They formed the new Seronera Pack, which survived until 1977; ♂ 16 remained subordinate.
2 sisters (♀ 45, ♀ 46) of the dominant ♀ and 3 younger adults (siblings, 1 ♀ and 2 ♂♂, 17-19 mo old) may have left the Genghis Pack together in 1975; ♀ 46 was seen alone 1 yr later.

5. Transfer under unknown circumstances

When histories of individuals were unknown, or when circumstances surrounding the transfer were unclear, movements of dogs between packs could not be classified into one of the above categories. However, Table 6 presents examples of unexplained transfers between groups where we knew that the ♂♂ and ♀♀ were not related to each other.

Table 6: Verified transfers of wild dogs, circumstances unknown, on the Serengeti Plains, Tanzania, 1968—1977. The ♀♀ were known to be unrelated to the ♂♂

6 ♀♀ (♀ 140, ♀ 141, ♀ 142, ♀ 143, ♀ 144, ♀ 145) joined Genghis Pack ♂♂, 1968.
4 ♀♀ (dominant ♀ 124 and daughters ♀ 122, ♀ 123, ♀ 25) from Herod Pack joined Plains Pack ♂♂, 1970.
1 ♀ from Herod Pack joined Flavian Pack ♂♂, 1971.
1 ♀ (♀ 25) from Nettle Pack joined Spitfire Pack ♂♂, 1971-1973.
1 ♀ (♀ 64) joined Kühme Pack ♂♂, 1973
2 sisters (♀ 19, ♀ 22) from Kühme Pack joined Falcon Pack ♂♂, 1977.

Correction to Table 6: Line 5 please read "1971—1974".

Most dominant breeding ♀♀ appeared to remain for life with the first male kin line they joined after leaving the parent pack. Two exceptions, one verified and one probable, were ♀ 1 and ♀ 22, each of which went with new ♂♂ following an invasion of their pack (Fig. 5). Although ♀ 1 eventually returned to her original mate, ♀ 22 did not (see section H.2.). In 2 other instances an adult breeding ♀ later became associated with a different pack (♀ 124 plus her 3 daughters of the Herod Pack between 1970—1971, and ♀ 25 with the Spitfire Pack between 1971—1974, Fig. 2). Circumstances of these transfers were unknown, but in each case subordinate ♀♀ were present the last time the pack was recorded intact. From the time each dominant ♀ was seen in a new pack, her former pack was never sighted again.

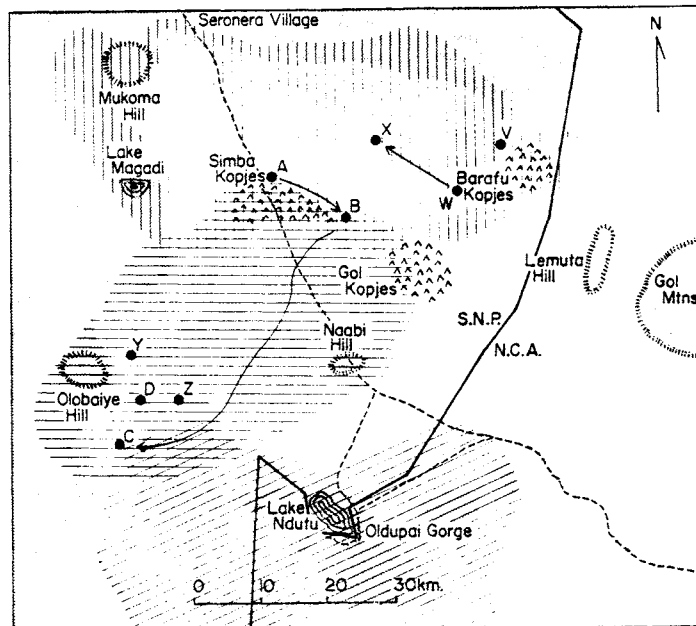
H. Behavior of emigrants

Two examples of primary emigration, observed as they happened, are described:

1. Emigration of 2 sisters

In February 1976, 2 sisters (♀ 19, ♀ 22) transferred from the Seronera Pack to the group of ♂♂ surviving from the Kühme Pack (Fig. 4). At the time of the emigration, the parent Seronera Pack consisted of a dominant pair, 1 subordinate old ♂, and 5 young adults from

the 1974 litter (3 ♂♂ and 2 ♀♀ just under 2 yrs old). The Kühme Pack remnant consisted of 3 adult related ♂♂ (♂60, ♂61, ♂62), each from a different litter; their breeding ♀ had disappeared 10 mo earlier.



PACK RANGE:

☐ Seronera ☐ Woodland habitat

☐ Kühme --- Road

☐ Spitfire S.N.P.-Serengeti National Park

N.C.A.-Ngorongoro Conservation Area

Fig. 6: Routes taken by 2 emigrating groups of wild dogs on the Serengeti Plains, Tanzania. Two sisters (♀19, ♀22): Point A — Seronera Pack and Kühme group near each other; B — sisters left their parent Seronera Pack; C — emigrating sisters joined the Kühme group (♂60, ♂61, ♂62); D — first den of the Kühme Pack after immigration of 2 sisters. Three brothers (♂34, ♂36, ♂37): V — Seronera Pack last seen intact; W — brothers left their parent Spitfire Pack and invaded the Seronera Pack; X — Seronera Pack's breeding ♀ (♀1) and Spitfire brothers last seen together; Y — Spitfire brothers seen with the Kühme Pack's sisters (♀19, ♀22); Z — first den of the new Falcon Pack

Observations were made 2 weeks prior to the emigration of the 2 daughters. Relations within the pack were amicable, and there was no unusual level of aggression directed to the young ♀♀. No ♀ exhibited signs of estrus.

Day 1: A herd of more than 1000 wildebeests passed southward (at Point A in Fig. 6). The 3 Kühme Pack ♂♂ were seen nearby. On the same day the Seronera Pack was seen less than 5 km away.

Day 2: The Seronera Pack was found less than 1 km from where the Kühme Pack ♂♂ were seen the day before. Two Seronera Pack ♀♀ were missing from their pack. The 2 packs may already have been in visual or olfactory contact.

Day 3: The Seronera Pack was again reported in the area, and continuous observation was begun. Both daughters (♀19 and ♀22) were absent from their pack, but they rejoined it that evening shortly after dark.

Both ♀♀ were behaving in an unusual way. Instead of following the lead of older pack members northward, they repeatedly made their own excursions south, sniffing the ground intently as they trotted. The rest of the pack continually returned to them. Or the daughters, harassed by spotted hyenas, returned to their pack. Repeatedly, ♀19 hoo-called; this vocaliza-

tion is made by wild dogs in distress, and is most frequently heard when pack members are lost or separated. She always called while looking south, sometimes even while standing in the midst of her parent pack. She then stood, ears alerted, staring south, as though waiting for some answer in that direction; we heard nothing.

The daughters remained in their parent pack through that night and the next, exhibiting the same restless behavior. The pack was under constant surveillance, and did not directly encounter any other dogs in that time. The dominant pair tried repeatedly to lead the pack northward, but the reluctance of the young ♀♀ to follow influenced the pack to stay on the southern edge of its range.

Day 5: On this morning the pack ate and rested (at Point B in Fig. 6). Both young ♀♀ still made brief excursions from the parent pack. At 07.30 h ♀19 ritual urine-marked in a patch of herbs 30 m from the parent pack. Neither she nor her sister had been seen before to raise a leg while urinating. Then ♀19 trotted away from the resting pack, leading southeast. She looked back and paused until her sister began to follow her. Both ♀♀ left and were not seen in the Seronera Pack again.

Except for a 9-h rest in the heat of the day, the ♀♀ traveled at a steady trot, with their heads low, as though following a scent trail. Occasionally they seemed to overshoot, and circled or zig-zagged with noses to the ground until the trail seemed to be found again. Throughout, ♀19 led and she alone gave hoo-calls. Often ♀22 lagged behind as she stopped to sniff the ground and roll in particular places. Once, in the evening, ♀22 urine-marked; ♀19 did not do so again during the emigration. The dominant status of ♀22 over her sister was occasionally but clearly demonstrated via ritualized gestures.

By 01.00 h the following morning they had covered a straight line distance of 65 km, most of it in an area in which their parent pack had never been seen to range. Then the sisters killed a wildebeest calf. After eating, they crossed a deeply-eroded river bed, and we lost them.

Day 6: At 08.10 h the ♀♀ were found 8 km further south. ♀19 stood hoo-calling, mainly in a northeast direction now, but her voice had become so hoarse that we doubted it carried over as long a distance as previously. The ♀♀ traveled slowly north 3 km in the morning, then lay down and rested until evening. That night they traveled south, then north again, arriving close to where they had rested the day before, having covered a further 10 km. They killed a wildebeest calf, ate, and then rested beside the carcass until dawn.

Day 7: At 07.10 h the ♀♀ fed a second time from the calf carcass, then set out northward. At 08.23 h, while running after 2 wildebeests with calves, the ♀♀ suddenly halted and looked northward. It appeared that the wildebeests had been running from 3 wild dogs now standing 150 m away (Point C in Fig. 5). They were the Kühme Pack's surviving ♂♂ (♂60, ♂61, ♂62). It was not clear where the ♂♂ had come from, but they were standing on the trail the ♀♀ had traveled the previous day. Possibly they were tracking the ♀♀.

The ♀♀ ran shoulder to shoulder toward the ♂♂, and the latter fled briefly. The 2 younger ♂♂ circled back toward the sisters when they were still 40 m away, and each met a ♀ nose-to-nose as she arrived. Each dog in the pair stood stiffly with head high and ears directed forward, throwing its weight behind head-thrusts at the partner. Nose-bumping and pressing against the partner's neck looked aggressive; yet lips were closed without any vertical retraction.

The ♀♀ took more initiative than the ♂♂, soliciting play by roughly pawing at head or flanks. Alternatively, the ♀♀ attempted to rear up on the ♂♂ or shove their nose into the groin. The ♂♂ were defensive, threatening with head and ear gestures, or more aggressively pressing the ♀♀ backwards with their nose against the neck. But neither ♂♂ ever reciprocated with an overt attack; when threats were not effective in repulsing the ♀♀, the ♂♂ terminated the interactions with abrupt spring-away cut-off gestures, or merely fled, with tail tucked. Repeatedly, the ♂♂ tried to get behind the ♀♀ to sniff or thrust heads into their groins.

The intensity of these interactions was unique, and their complexity made them difficult to classify. The type of interaction they most closely resembled was courtship. Yet behavior in this initial encounter between potential mates was ambivalent, a character not seen between courting wild dogs that know each other well. Using this interpretation of the behavior we saw, we term it *trial courtship*.

All trial courtship and gestures of dominance and subordination that occurred among the 5 dogs during the 16 h of daylight observations subsequent to their joining are diagrammed in Fig. 7. There was a qualitative difference in the courtship gestures used by ♂♂ and ♀♀, in that ♀♀ frequently used play solicitation and active appeasement in their approaches, whereas ♂♂ usually did not. The dominant ♂ was initially as attracted to one ♀ as the other. But it was not clear whether the sisters directed most of their attention to him because of preference, or because he was so effective at excluding the other ♂♂.

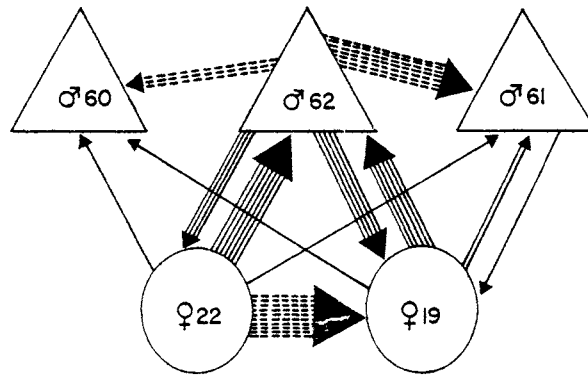


Fig. 7: Sociogram of dominance relationships and trial courtship that occurred when 2 sisters joined the 3 Kühme ♂♂ in February 1976. Dashed vector = *dominates*, and solid vector = *initiates trial courtship*; one line represents 1–10 interactions and each additional line is 10 interactions

The 3-yr-old dominant ♂62 threatened ♂61 away from both ♀♀ within the first min of their arrival. Thereafter ♂61 and the older ♂60 remained peripheral. And ♀22 threatened and attacked her sister whenever the latter was near any ♂.

Only the dominant ♂ attempted to mount the ♀♀. His first attempt was seen within 30 min of their joining. In 16 h, ♂62 attempted to mount ♀19 12 times, and ♀22 17 times.

The dominant ♂ urine-marked several times, about 1½ h after first meeting. Finally ♀22 covered his mark while her sister stood nearby, intently sniffing the mark. Afterwards ♀19 rolled on the place, but did not attempt to mark there. The subordinate ♀19 urinated once elsewhere with alternate hind legs raised, but was not seen marking again thereafter.

Dominant ♂62 and ♀22 urine-marked together 7 more times. Frequently ♀22 rolled on the ♂'s mark before urinating there. Twice she defecated on the urine marks afterwards. The ♂ urine-marked alone an additional 7 times, and ♀22 alone an additional 2 times.

Interaction rate between the dominant ♂ and both ♀♀ remained high for the first morning and evening's activity periods. By the next morning, interaction rate had dropped to half (to about 1 per min), with nearly all social interaction limited to these 3 individuals. Interactions were similar to those of the day before.

The 5 dogs hunted together the first evening, and again the next morning. The 2 younger ♂♂ selected and captured the prey, in both instances a wildebeest calf. The ♀♀ helped during the kills, and ate with ♂62. The 2 subordinate ♂♂ were threatened off the kills, apparently because of their proximity to the ♀♀. We terminated observations at midday, 26 h after the dogs met.

The new pack was seen 3 more times in the next 5 mo, ranging within the Kühme Pack's known area. At the end of that time ♀22 had her first litter (at Point D in Fig. 6). ♂62 was still dominant and the presumed father of the puppies. The subordinate ♂61, then 8 yrs old, had disappeared, and presumably died. The subordinate ♀19 showed no signs of pregnancy.

2. Emigration of 3 brothers

In March 1977, we observed 3 brothers (♂34, ♂36, ♂37), 2½ yrs old, as they emigrated across the ranges of 2 other packs (Fig. 6).

We had last seen the 3 brothers' parent Spitfire Pack in January, when it was still intact and contained 2 old adult ♂♂, the 3 brothers and 1 sister, and their mother who had another litter of 10 pups (7 mo old). The 3 young adult ♂♂ constituted the pack's main hunting strength, and their departure may have had serious consequences for the parent pack.

The 3 ♂♂ invaded the Seronera Pack in March. This pack consisted of a breeding pair and 1 older subordinate ♂, and was last seen intact 3 days earlier in the northeastern part of its range (Point V in Fig. 6).

The dominant ♀ of the Seronera Pack was found alone 3 days later (at Point W in Fig. 6), 2 km from the last sighting. She (♀1) was trotting west, frequently stopping to hoo-call. After 5½ km she passed within 100 m of the 3 ♂♂ of the Spitfire Pack. The Spitfire Pack was never seen within 30 km of this point, and the center of their home range was 60 km away. The 3 ♂♂ were resting, and watched the ♀ go by. For wild dogs to ignore a conspecific was very unusual, so we assumed that the 4 dogs had been in contact already.

About 1½ km beyond these ♂♂, the ♀ met ♂16, the older subordinate ♂ of the Seronera Pack. He had a fresh wound in his abdomen, through which his viscera protruded. His behavior, although sluggish, was not greatly impaired. He moved to the ♀ to greet her. Then he put his chin on her back and leaned, as though intending to mount. The ♀ resisted and moved away from him. She continued to hoo-call. Both dogs rested during the heat of the afternoon. Occasionally both stood and hoo-called. There was no sign of the dominant ♂ of the Seronera Pack. Twice more the ♀ avoided ♂16 when he approached to nuzzle or groom her.

That evening, as the Seronera Pack's ♀ and ♂ stood hoo-calling, the 3 ♂♂ of the Spitfire Pack arose and ran toward them. Immediately ♂16 rolled over and lay motionless in complete passive submission. The 3 ♂♂ trotted close and looked at him, but almost at once turned their attention to the ♀, who ran to greet them. Then ♂37, most subordinate of the 3 ♂♂, was noticed to have a fresh cut on his flank. The ♂♂ returned the ♀'s greeting.

Within the first min after the greeting, ♂36 and ♂37 suddenly withdrew from the ♀, probably at a threat from the dominant ♂34. The ♀ and ♂34 were then left sniffing each other, and they soon began interacting at a rapid rate. The ♀ initiated most interactions, making intense gestures of play solicitation and active appeasement. The ♂ responded with attempts to sniff her anal or genital region, or to mount. None of the ♂♂ initiated many social interactions with her. She interacted almost exclusively with the dominant ♂. A sociogram of trial courtship and gestures of dominance and subordination seen among the 4 dogs in the subsequent 13½ h of daylight observations is shown in Fig. 8.

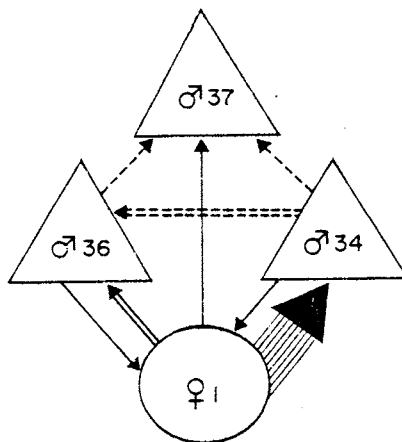


Fig. 8: Sociogram of dominance relationships and trial courtship that occurred when 3 brothers invaded the Seronera Pack and took over its breeding ♀ in March 1977. Dashed vector = *dominates*, and solid vector = *initiates trial courtship*; one line represents 1—10 interactions and each additional line is 10 interactions

As in the immigration of the 2 ♀♀ into the Kühme Pack in 1976, it was unclear whether the new ♀ directed most of her attention to the dominant ♂ because of preference, or because he prevented access to the other ♂♂. Synchronous urine-marking between ♂34 and the ♀ was first seen 3½ h after the 4 dogs met that evening. No other ♂♂ attempted to mark. However, the second-ranking ♂ mounted the ♀ several times during travel, when the dominant ♂ was far ahead of the others.

When the ♀ and the 3 brothers began traveling that evening, ♂16 was left behind. He was never seen again, and is presumed to have died of his wound. The proximity of the 2 packs, the fact that ♂♂ in both packs were wounded, and the absence of the dominant ♂ of the Seronera Pack strongly suggest that the 3 young adult ♂♂ forcibly disrupted the Seronera Pack.

The ♀ of the Seronera Pack quickly took leadership of the group's movements, and continued traveling after dark. She still hoo-called. As she led she seemed to follow scent trails occasionally, and apparently she was searching for her mate. The brothers frequently lagged, and all the dogs looked tired when they stopped to rest shortly before midnight. When the dogs resumed traveling at dawn, behavior was similar to that of the day before. Observations ended shortly before noon, by which time the pack had traveled 44 km (to Point X in Fig. 6).

The 3 brothers reappeared 10 days later (at Point Y in Fig. 6). With them were the 2 ♀♀ from the Kühme Pack — ♀19 and ♀22. The Kühme Pack was seen intact 2 mo before with these 2 ♀♀, 2 adult ♂♂, and 8 large pups (born to ♀22). The 3 Spitfire ♂♂ may have invaded the Kühme Pack and taken the ♀♀, but this was not verified.

We saw ♀22, still dominant over her sister, urine-marking with ♂34. The new group of 5 dogs was seen several times (in the area around Point Y in Fig. 6) during the next 2 wks, then ♀19 disappeared. About 3 mo later ♀22 denned (at Point Z in Fig. 6). This new breeding unit was named the Falcon Pack (Fig. 5).

About 9 wks after ♀19 disappeared from the new Falcon Pack, she was found with ♂62, the dominant ♂ of the Kühme Pack. She was heavily pregnant. The old ♂ and the large pups of the Kühme Pack were not seen again, so all were presumed dead because they were unable to hunt for themselves. These dogs may have died before the 3 brothers appeared and joined (or abducted) ♀19 and ♀22.

The breeding pair of the Kühme Pack (♀19 and ♂62) was not seen again. It is unlikely that they raised pups, because we have no records to indicate that 2 adults alone can rear pups through the whole year of dependency.

The 3 brothers' effect on the Seronera Pack was clearer. One month after their invasion, the ♀ of the pack was seen back with her original mate, ♂17. The ♂ had no obvious wounds, but he was listless, shaky on his feet, and had diarrhoea. About 6 mo later, at the start of the wet season, we found ♀1 alone in her usual range. We concluded that her mate must have died. She looked thin and was losing her kills to spotted hyenas. However, she survived on her own through the subsequent 6½ mo of prey abundance. At last sighting, in June 1978, she looked healthy.

The effect of the 3 emigrating ♂♂ on the breeding population as a whole was significant. The viability of 2 of the 5 resident packs was destroyed. The 3 brothers' own parent Spitfire Pack may have suffered because of their leaving it. And the newly formed Falcon Pack, while establishing a new home range in the center of the study area, several times was seen attacking the Plains Pack, apparently displacing them further to the east. The new Falcon Pack also contributed to the death of a small pup of the Plains Pack's 1977 litter when they attacked and separated the adults from the pups for at least 2 days.

I. Mechanisms facilitating emigration and transfer

Trial courtship behavior was seen in all of 6 packs we observed within 2 wks of the arrival of new ♀♀. The ♀♀ were markedly active in play and sexual solicitation, behavior extremely effective in subverting possible aggression from strange ♂♂, and in aiding rapid integration with them. Such functions are suggested because the mounting and thrusting behavior in the newly formed packs we saw often did not lead to conception, and there is no evidence, except in cases of pack fission, that emigrating ♀♀ were in estrus at the time they left their former packs. Of 8 breeding ♀♀, 4 did not conceive until 10—12 wks after joining new ♂♂. The only cases of almost immediate conception (less than 2—3 wks) occurred where the breeding pair already knew one another, as in pack fission, and in the case of the subordinate ♀19 returning to mate with the dominant ♂62 of the Kühme Pack.

The 2 daughters of the Seronera Pack appeared to emigrate voluntarily, i.e. the ♀♀ were not expelled from their parent pack. The proximity of a breeding opportunity apparently precipitated their departure and subsequent search. If the 2 packs did not actually meet, the ♀♀ probably learned of the presence of the ♂♂ via scent marks. Their behavior suggested that they were following this specific group of ♂♂.

By contrast, the 3 sons of the Spitfire Pack probably did not know of the existence of the Seronera Pack ♀ until after they left their parent pack's range. Similarly, 4 ♀♀ from the Seronera Pack (Fig. 4) in December 1974 emigrated and wandered 3½ mo before joining the surviving Plains Pack ♂♂. These examples, plus the abrupt disappearances out of the study area of other dogs (Tables 2—4), suggest that some dogs emigrate independently of known opportunities to breed.

Behavior of the 3 brothers from the Spitfire Pack indicated that violent transfers are an alternative strategy. The emigrating ♂♂ attacked dogs of the same sex in an existing breeding unit. In the one verified and several suspected cases of male invasion with abduction of the ♀, the invading ♂♂ outnumbered the incumbents. The remnant of the Kühme Pack, 2 vigorous ♂♂ and 1 very old ♂, did not attack the larger Seronera Pack; the 2 daughters of the Seronera Pack emigrated to them.

Most wild dogs emigrated when prey was abundant on the plains. The month of emigration or disappearance was known for 53 of 74 adults. Of these 53, 42 (79%) emigrated or disappeared from January—April, the months with the heaviest rainfall and most abundant prey. No individuals emigrated or disappeared from August—October, the driest months. In the rainy season, heavy localized concentrations of wildebeests often attracted 2 or more packs of wild dogs, increasing both direct and olfactory contact, and facilitating transfers. Abundant, easy-to-catch prey allowed small emigrating groups, such as the 2 sisters from the Seronera Pack, to survive during the transfer. These conditions also permitted immigrants to be integrated into the hunting of a pack before the more rigorous conditions of the dry season prevailed.

More frequent contacts between packs in the rainy season, however, could increase the transmission of contagious diseases, e.g. canine distemper. This could explain some of the disappearances, especially of dogs 12—14 mo old.

V. Discussion

The typical wild dog pack comprised 2—6 related adult ♂♂ (often from more than one generation), 1 or several adult ♀♀ (who were sisters, but not related to the adult ♂♂), and pups or young adults who were born in the pack. This pack composition was a result of (1) ♂♂ usually remaining with other male relatives, creating male kin lines that were often continuous over many years, and (2) ♀♀ emigrating, first from the parent pack (primary emigration), and then from each other (secondary emigration).

A consequence of emigration is that close inbreeding is avoided. Despite the small size of the breeding population studied, no closely related wild dogs were known to have mated with each other. At least one vertebrate is known, the Mexican jay (*Aphelocoma ultramarina*), where the costs of dispersal are so high that close inbreeding may have arisen (BROWN 1974). Wild dogs exist at very low densities over much of their range, and dispersing individuals or groups might have great difficulties in locating packs. If persistent close inbreeding were to occur, with a concomitant increase in genetic relatedness between pack mates, there might be dramatic effects on the social organization by lowering the levels of competition between ♀♀. Where ecological conditions permit, multiple, synchronous denning by several ♀♀ in each pack might result.

A. Evolutionary considerations

Wild dogs on the Serengeti Plains subsist at all times of the year by the cooperative hunting of large prey. Their system of group hunting is very effective, and the advantages to the individual living in a group are clear.

Like other canids, wild dogs produce altricial young that require high levels of post-natal investment. For wild dogs, group hunting of large, fast prey with its strenuous demands on endurance and skill has further increased

the period of juvenile dependency. All the adults in a pack, while benefiting from group hunting, are available all year round to provide food for the lactating ♀ and her pups. The breeding members of a pack appear to have exploited the advantages of group living. The very large litter size, which is almost twice as large as that of closely related species, means that a single breeding pair can monopolize the reproductive effort of a whole pack.

Subordinate dogs within the pack have less reproductive success than dominants. Besides trying to raise their own pups in the pack where they are not dominant, subordinate dogs have 2 other ways in which to increase their fitness. They can

(1) increase their inclusive fitness by helping to raise young born to the dominant breeding pair, or

(2) leave the pack and seek breeding opportunities elsewhere.

During the study most non-reproductive "helpers" were ♂♂, while most individuals that sought breeding opportunities through emigration were ♀♀. The ability to invest in pups and the capacity for group hunting seem to be equally well developed in both sexes. It is therefore unlikely that ♂♂ remain because they can contribute more to the raising of pups. Also, the advantages to a ♂ that can monopolize the reproductive effort of a whole pack would appear to be identical to those accruing to a single breeding ♀.

However, a dominant ♀ probably stands to lose more if a subordinate ♀ tries to breed, than a dominant ♂ does from rival breeding ♂♂. First, if a subordinate ♀ produces pups at a different time than the dominant ♀, the pack is restricted to a limited part of its range for a longer period each year. For a species that lives on prey scattered over a very large home range, this has disadvantages for all individuals in the group (KLEIMAN and EISENBERG 1973).

Second, if 2 adult ♀♀ reproduce at the same time, there is direct competition for the investment provided by the adult members of the pack. If pups from 2 litters survive, they all suffer reduced nutrition, and it is common for the pups of the subordinate ♀ to be eliminated in the course of a protracted and wasteful contest. Also, ♀♀ fight for access to pups, and neither mother will leave her pups unattended in the presence of the other mother. With 2 ♀♀ to be provisioned at the den, nutrition is further reduced, and lactation may be impaired.

In contrast to this, reproductive competition between ♂♂ is expected to have less serious consequences on the reproduction of a pack. First, competition between adult ♂♂ to inseminate a single ♀ occurs before the pups are born, and therefore does not interfere with the amount of investment provided for the pups that are produced.

Second, in some packs subordinate ♂♂ were seen mating with the dominant ♀ before the dominant ♂ copulated with her. It seems possible, therefore, for more than one ♂ to sire a litter. Such uncertain, possibly mixed paternity may help to maintain male groups.

Of less certain importance is that among ♂♂ there is lability of dominance status. (Relative lability of female dominance is unknown, because ♀♀ did not remain together long enough for the comparison to be made.) This lability makes it possible for the sons or brothers of the dominant breeding ♂ to assume alpha status at a young age, without having to emigrate.

In combination these 3 factors may influence the maintenance of cooperating male groups. Young ♂♂ are more likely than young ♀♀ to achieve breeding success without emigrating. ♀♀ compete for access to these groups of ♂♂.

The basic difference in the form of reproductive competition between $\delta\delta$ and ♀♀ when reproduction depends on *depreciable* investment (ALTMANN, WAGNER and LENINGTON 1977) has a number of important consequences. The advantages of group hunting, as well as the benefits of having a single breeding ♀ can be realized in the formation of groups of cooperating $\delta\delta$. The necessity for close cooperation between adult $\delta\delta$ probably explains the amicable relations that usually exist in wild dog packs. Selfish tendencies are also mitigated by the close ties of kinship. The risk of occasional sexual access of subordinate $\delta\delta$ to the dominant ♀ is the price the alpha δ has to pay to insure the investment of the pack in young, the majority of which he will probably sire (VEHRENCAMP in press).

B. Effects of the declining population

Male recruitment and female emigration were seen consistently throughout the study. The decline in the population probably accentuated the basic pattern of male recruitment and female emigration in at least 3 ways:

First, as pack size declined because of low pup survival, the few male littermates that survived tended to remain in their parent packs. The primary emigration of male littermates occurred only when 3 or more $\delta\delta$ from a single litter survived. Some factors that may influence sons to emigrate rather than be recruited are (1) the emigrating groups are large enough to form permanently independent hunting units, (2) the number of rival $\delta\delta$ in the parent pack is high enough that emigration offers a higher chance of breeding success than recruitment, and (3) the parent pack is so large that recruitment would be a liability to members in terms of food competition.

Second, as mean pack size declined, subordinate ♀♀ were forced to undergo secondary emigration without $\delta\delta$. Thus, very little pack fission was observed. Significantly, the 3 recorded cases of pack fission, where a separate breeding unit split away from a large pack, all occurred before 1972 in packs that contained 7 or more adult $\delta\delta$.

Third, as a higher proportion of $\delta\delta$ remained in their parent packs, the opportunities for emigrating ♀♀ to reproduce were further reduced. These ♀♀ tended to be alone or in groups of 2 when undergoing secondary emigration, so failure to quickly join $\delta\delta$ resulted in increased mortality (or emigration out of the study area), contributing to the radically skewed sex ratio in older adults of 3 $\delta\delta$ to every ♀ . This loss of ♀♀ , by reducing the number of unattached ♀♀ available to emigrating $\delta\delta$, would further reinforce the pattern of male recruitment.

The low density may also have created conditions for male invasion. In the documented case, 3 $\delta\delta$ were able to disrupt 2 different packs and abduct their ♀♀ , all within 10 days. It seems likely that if there had not been such low pup survival, the $\delta\delta$ would not have found small packs that were susceptible to disruption. In an increasing or dense population, groups of emigrating $\delta\delta$ would be more likely to meet unrelated emigrating ♀♀ , than to forcibly break up existing packs.

We hypothesize that a larger mean pack size (i.e. greater pup survival) would result in more cases of pack fission, more cases of male primary emigration, more and larger groups of free-roaming female littermates, and less pack invasion by $\delta\delta$ than we noted during the study. The underlying pattern of male recruitment and female emigration would probably remain the same in this sub-population. The degree to which these wild dogs have scaled their

social organization to exploit a difficult habitat will become clear only after studies of wild dogs in other habitats are completed.

Summary

African wild dogs (*Lycaon pictus* Temminck 1820) were studied on the Serengeti Plains, Tanzania, from 1967 to 1978. Each pack ranged over an area of approximately 1500—2000 km², and shared parts of its range with neighboring packs. The sub-population declined from 95 to 26 adults (from 12 to 7 packs) during the 10½ yrs, resulting in a density of 1 adult/200 km² in 1977. *Pack* is defined as a real or potential breeding unit. The typical pack consisted of related adult ♂♂, at least 1 unrelated adult ♀, and pups. *Group* is defined as a pack, lone dog, or any other association. Mean group size over the entire study period was 9.8 (range 1—26), and mean adult group size was 6.0 (range 1—18); 92% of the groups were breeding units. The decline in the sub-population resulted in fewer breeding units and decreased mean group size. The sex ratio was biased with 59% male pups less than 1 month old, 64% male adults (1—11 yrs old), and 75% male adults (more than 5 yrs old). Of 26 observed natal dens, the dominant ♀ whelped at 20 and a subordinate ♀ whelped at 6. Only one of the 6 litters born to subordinate ♀♀ survived to adulthood; this litter was born at a den where the subordinate ♀ whelped at a different time from the dominant ♀. Mean litter size was 10.1 (range 6—16). Packs changed in adult composition other than by deaths in 4 ways: Recruitment of juveniles born in the pack; dispersal of young from the parent pack with transfer to another group; dispersal of subordinate adults from a pack (not their parent pack) with transfer to another group; and pack fission, where two new breeding units were formed from one pack. The pattern most frequently seen was male recruitment and female emigration. No ♀ remained in her natal pack, but 2 male kin lines persisted for at least 10 yrs. Emigrants left packs in which there was a dominant breeder of the same sex, and siblings of only the same sex emigrated together. One group of emigrating ♂♂ violently disrupted at least one breeding unit. Pack fission was the phenomenon in which at least 1 ♂ and 1 ♀ (unrelated to each other) left a pack together to breed. Behavioral details are given for an example of female emigration, and an example of ♂♂ invading an existing pack and taking over the dominant breeding ♀.

Zusammenfassung

Afrikanische Hyänenhunde (*Lycaon pictus* Temminck 1820) wurden in der Serengeti-Steppe Tansanias von 1967 bis 1978 beobachtet. Jedes Rudel bewohnte ein Gebiet von ungefähr 1500—2000 km², das teilweise mit denen der benachbarten Rudel überlappte. Die Teilpopulation sank während der 10½ Jahre von 95 erwachsenen Tieren auf 25 (von 12 Rudeln auf 7) ab, was 1977 einer Dichte von einem erwachsenen Tier pro km² entsprach. *Rudel* ist definiert als echte oder potentielle Fortpflanzungseinheit. Das typische Rudel besteht aus verwandten erwachsenen ♂♂, mindestens einem nicht verwandten erwachsenen ♀ und den Jungen. *Gruppe* ist definiert als Rudel, einzelnes Tier oder jede andere Gemeinschaft. Die mittlere Gruppengröße über die gesamte Beobachtungszeit hinweg betrug 9,8 (1—26), die von Erwachsenengruppen 6,0

(1—18); 92% der Gruppen waren Fortpflanzungseinheiten. Die Abnahme der Teilpopulation hatte weniger Fortpflanzungseinheiten und eine geringere Gruppengröße zur Folge. Das Geschlechtsverhältnis war ungleich, mit 59% ♂♂ unter einem Monat, 64% erwachsenen ♂♂ von 1—11 Jahren und 75% über 5 Jahre. In 20 von 26 beobachteten Bruthöhlen warf das dominante ♀ Junge, in 6 das subdominante. Nur einer von 6 Würfen unterlegener ♀♀ überlebte; er wurde in einer Höhle geboren, in der das überlegene ♀ zu einer anderen Zeit Junge hatte. Die mittlere Wurfgröße betrug 10,1 (6—16). Die Zusammensetzung der erwachsenen Rudelmitglieder änderte sich außer durch Todesfälle auf vier Arten: 1. Eingliederung der im Rudel geborenen Jungen, 2. Auswandern der Jungen aus dem elterlichen Rudel und Anschluß an eine andere Gruppe, 3. Auswandern von unterlegenen erwachsenen Tieren aus dem Rudel (nicht dem elterlichen) und Anschluß an eine andere Gruppe, 4. Aufspaltung des Rudels in zwei neue Fortpflanzungseinheiten. In der Regel wurden die ♂♂ eingegliedert, während die ♀♀ auswanderten. Kein ♀ blieb im elterlichen Rudel, aber zwei männliche Verwandtschaftslinien bestanden mindestens 10 Jahre lang. Auswanderer verließen Rudel, in denen ein überlegenes Tier des gleichen Geschlechts sich fortpflanzte, und nur gleichgeschlechtige Junge wanderten miteinander aus. Eine Gruppe wandernder ♂♂ sprengte gewaltsam mindestens eine Fortpflanzungseinheit. Bei Aufspaltung eines Rudels verließen mindestens ein ♂ und ein nicht verwandtes ♀ gemeinsam das Rudel und bildeten eine neue Fortpflanzungseinheit. Eine Auswanderung von ♀♀ und das Eindringen von ♂♂ in ein bestehendes Rudel mit Übernahme des dominanten ♀ sind im einzelnen beschrieben.

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