

Pack formation, protocols of social behaviour and conservation of the African Wild Dog (*Lycaon pictus*)

Roger Burrows (October 2002) Revised June 2011

Lycaon is a highly social, medium sized canid endemic to Africa where it lives in packs. The simplest pack comprises a lone pair of usually unrelated individuals plus or minus their offspring living on a home range. However, most packs consist of a dominant (alpha) breeding pair and their offspring, accompanied by subordinate same sex adult relatives of either or both of the alpha pair and sometimes offspring of one or more subordinate pairs. Totally unrelated individuals or groups of either sex may sometimes join such packs, usually temporarily.

Although formerly widely distributed, to-day occurs in two main areas with contrasting habitats:-

i. East Africa : in dry savannah and seasonally flooded grasslands, with annual concentrations of migratory antelope prey species. These are probably *Lycaon*'s original habitats, occupied for at least the last 1MY.

ii. Southern Africa : in low altitude 'Mopane' (*Colophospermum*) and 'Zambeziian' (*Acacia*, *Combretum*, *Terminalia*) woodlands and seasonally waterlogged or flooded grasslands often bordering permanent rivers e.g. Kruger NP, Luangwa NP, Moremi GR. Here *Lycaon* is highly dependent on Impala, a prey species which, although having the advantage of being highly residential and existing locally at high densities year round, has very special habitat requirements.

Fire degraded deciduous moist woodlands such as the 'Miombo' (*Brachystegia*) covering much of the poor soil areas of southern Tanzania and most of Zambia, is not typical *Lycaon* habitat. Its distribution in such areas is confined to 'edges' (ecotones) between natural grasslands and woodland in ancient wide valleys where perennial rivers flow through the miombo e.g. Northern Selous GR., Ruaha NP. The distribution of *Lycaon* in large areas shown as 'miombo woodland' on maps is therefore, like that of its main prey the Impala an ecotone species, very irregular and clumped.

'Serengeti' (i.e. the Tanzanian sector of the Serengeti-Mara ecosystem) savannah packs den in widely scattered locations in the summer wet season when water is normally widely available in a plethora of temporary pools/water courses. Woodland packs den in the winter dry season when not only prey but *Lycaon* and other predators are concentrated around the limited remaining permanent water e.g. Moremi GR and Kruger NP.

Based on morphological differences, genetic variation and habitat occupied, it was formerly claimed that the East African and southern African *Lycaon* populations were two distinct geographically isolated subspecies (Girman et al 1993). Now based on further mtDNA analysis, and disregarding any morphological, habitat or possible behavioural differences between the two populations, it is suggested that two sub species probably do not exist but that there are merely two genotype clades (Girman et al 2001).

However another study using similar mtDNA techniques related to possible speciation in the Crossbill (*Loxia*), recommends that such modern genetic techniques should be used in conjunction with the more traditional methods of defining a species such as those based on behavioural and ecological studies (Piertney et al. 2001).

A resolution to this sub species issue is urgently required as it has very important implications for the management and conservation of *Lycaon*.

Two major questions need to be urgently resolved: -

i. Despite recent claims to the contrary based on genetic evidence only, do any behavioural differences suggest the existence of two separate sub species of *Lycaon*, one in East the other in southern Africa?

ii. Do the social protocols of 'Serengeti' *Lycaon* packs living in open savannah habitat where trees and thick bush are actively avoided also apply generally to other populations in wooded/ bush habitats?

Are there behavioural differences between East African and southern African *Lycaon* populations?

An answer to this question will depend on whether the behavioural protocols, which are the basis of male and female dominance hierarchies in the East Africa Serengeti population and so control the formation,

maintenance and dissolution of both free living and captive packs, also apply generally in southern African populations. It is essential that the answer is known if attempts to conserve this endangered species and maintain genetic diversity in the species are to be successful.

Since 1990 a 'growth industry' in *Lycaon* research and publications has existed. However it is evident from the many recent publications on *Lycaon*, that most authors writing on the behaviour of, and attempts to conserve, this highly endangered species apparently have so far failed to recognise the existence of two basic protocols of *Lycaon* society in East Africa, 'youth first' and 'leadership' (Burrows 1995, Visee et al. 2001). There is therefore a lack of awareness that these same protocols explain much of the behaviour reported in other free living and captive populations.

The apparent lack of understanding of all the known social behaviour protocols which underlie the formation and maintenance of successful free living packs, has led to the release of miscellaneous collections of individuals of different ages and relationships, as 'packs', into various game reserves in southern Africa. This has almost always proved disastrous due usually to the social incompatibility of their members, with most such artificial 'packs' dying from disease, lion predation, or not breeding and disintegrating into sub-units (Woodroffe 1997, Hofmeyr 2001).

Unless this situation is quickly corrected many current conservation measures in protected areas, including often controversial re-introductions and translocations, will inevitably lead to failure, and perhaps result in unacceptable levels of *Lycaon* mortality and loss of genetic variability.

Basic protocols in *Lycaon* social behaviour in East Africa

Based on data collected by various researchers over the period 1964-91 in 'Serengeti' (Tanzania, East Africa), and a review of the literature on free living and captive study populations in other areas/habitats in Africa, in all cases where the age and relationship of the individual *Lycaon* are accurately known, two basic social protocols emerge.

1. The 'Youth First' protocol in the *Lycaon* male social hierarchy: -

In a pack when either of the alpha pair of dogs dies the pack breaks up into separate single sex groups (i.e. pack dissolution). In the resulting all-male group, which remains resident in the former pack's home range, a member of the youngest cohort present will emerge as the new alpha male in the social hierarchy when new females join the male group. Assumption of alpha status by the younger individual appears to take place without overt physical aggression. This behaviour is probably unique in social mammals.

The 'youth first protocol' is now known to have applied in a wide variety of male groupings

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- i. in free living packs when groups of males of mixed cohorts dispersed in 'Serengeti' (Nicholls 1990, Burrows 1995 c.f. Scott 1992)
- ii. in a free living pack in Kruger NP (Reich 1981).
- iii. when free living older males adopt a younger male(s) (McNutt 1996a).
- iv. in wild born and younger captive born males in captivity (Visee et al 2001).
- v. in an artificially constructed mixed age group in captivity (van Heerden &Kuhn 1985).
- vi. in a released group of captive bred, hand reared individuals with older wild bred males (Hofmeyr 2001).
- vii. and probably in some woodland packs where all male groups or individuals remained in their natal home range following the loss of the breeding female from their pack (McNutt 1996b).

The same 'youth first' behaviour with a male from the youngest cohort present becoming alpha in such disparate groupings of males and varying natal origins suggests that such behaviour has a genetic basis.

2. Protocol in Leadership

A wild dog will accept as leader of their pack or group: -

- i. Their parents whilst both are present in the pack.
- ii. A same sex member of their litter in a single sex group
- iii. A younger brother (or son in the case of a former alpha) in an all male group.
- iv. The alpha female in a dispersing mixed age group of females (i.e. alpha female's offspring) following pack dissolution. This has also recently been reported to apply to study packs in Moremi G.R., Botswana, (John McNutt pers. comm. 2005)
- v. Recently it has been reported that the 'Youth First Protocol' applies not only to males in Moremi G.R. study packs but also to dispersing groups of female sisters of mixed cohorts with a younger female becoming alpha (John McNutt pers. comm. 2005).
- vi. An unrelated younger male in the case of a male group adopting pups (McNutt 1996).

It is probably mainly for these reasons that *Lycaon* has never allowed itself to be domesticated. Based on the basic protocols of 'Youth first' and 'Leadership', both the structure of free living packs and the often dramatic and sudden changes in their composition over time can be explained. The existence of these protocols also explains why, if not followed, as is the case in most artificially constructed packs, high levels of aggression and mortality occur in captive packs and why those 'packs' introduced to the wild usually disintegrate.

THE LYCAON PACK:

Packs may contain just a single breeding pair or over 40 individuals including the dominant (often referred to as the alpha pair), and one or more subordinate breeding pairs. Two or more litters are reported to have been raised successfully in some *Lycaon* packs in a single annual breeding season.

When other (i.e. non dominant) founder adult member of each sex are also present (i.e. in starter packs and recently formed 'resident packs' some authors report that separate male and female hierarchy exists (e.g. H.& J. van Lawick -Goodall 1970, Creel & Creel 2002) by contrast McNutt & Boggs (1996) refer only to a dominant pair and the rest of the pack as subordinates.

Amongst the subordinates there is however an obvious difference in the priority of access when feeding at a pack kill. After the kill those adult involved quickly feed on easily snatched viscera, but as soon as the rest of the pack arrive they step aside and allow any pups to feed sometimes with the alpha female although the pups attempt to interfere with her feeding. Once satiated any yearlings present feed again sometimes reluctantly sharing the prey with the alpha female. Only when all the younger cohorts have fed do any older subordinate adults (i.e. subordinate founder pack members) feed if sufficient food remains. Unlike most other large carnivores there is therefore a feeding order in wild dog packs based on age.

Whatever terminology is used, all subordinates i.e. founder adults of both sexes and those born in the pack defer to the dominant pair.

The males in the pack are usually all related to each other, as are the females in the packs, but the males and females are usually not closely related. Other related or unrelated adults of either sex may sometimes join the pack but usually do so only on a temporary basis.

Strong social bonds exist, perhaps for life, between same sex members of a cohort, so in a pack a number of single sex sub groups exist simultaneously. The alpha pair acts as a unit of social cohesion, or 'glue', holding this loose federation of units of different cohorts together as a pack. When either of the alpha pair dies the 'social glue' fails and the pack breaks up into an adult male group and one or more female groups including the old alpha female if she is the survivor, which go their separate ways in their quest for new partners.

Consequently any 'natural' (e.g. due to lion predation, injury leading to starvation, or pathogens), or human intervention (e.g. snaring, shooting or routine immobilisation of individuals as part of scientific research or for translocations) which deliberately or inadvertently leads to the death of either of the alpha pair will cause pack dissolution and increase social instability in the population.

If the alpha female dies the alpha male immediately loses his social status. A son from the youngest cohort present becomes the new alpha with all the older males, including the former alpha if he has survived, remaining in the resulting all male groups as subordinates.

The alpha female retains her position in a pack only whilst her mate is also present. However, if she survives the death of her partner, she retains her alpha social position over her same age sisters and female offspring in any dispersing female group of which she is a member.

If two cohorts of female siblings disperse together following dissolution of their natal pack then it has recently been reported that one from the youngest cohort becomes dominant in the group and any new pack they subsequently help to form (John McNutt 2005). The separate male and female groups resulting from pack dissolution already have a dominant although this individual is not always apparent by their behaviour in the single sex groups before they meet to form a new pack. The dominant pair however immediately become apparent to observers when a new pack is formed (Frame & Frame 1986). Close observation of the behaviour and interactions with other pack members of potential emigrants before they leave their natal packs also allows the identification of the young dominants of each sex in their cohort.

PACK FORMATION AND SIZE

It is important to recognise that the size and composition of 'new' packs will vary considerably depending on the size of the male and female groups which join to form the pack. It is however important to distinguish between what may be termed 'Starter' and 'Resident' packs.

'Starter pack'

This is a potential breeding pack formed when a lone or group of dispersing males meet a lone or group of dispersing females to which the males are usually not closely related and then attempt to establish a home range in an area which may not be near either groups natal pack's home range.

It is reported that particularly in woodland habitats such interactions between dispersing groups often fail to lead to a stable pack with the small groups, or single individuals of either sex separating again soon after meeting with sometimes the females returning temporarily to their natal pack or single male dying or disappearing (McCreery & Robins 2001, McNutt 1996)

Usually all the individuals in such packs will be older yearlings (i.e. 18-24 mo.) with an established dominant in each group and so the alpha pair immediately become apparent when the groups meet. Based on the 'Leadership' protocols above, if more than one cohort of males is present in the dispersing group then a male from the youngest is alpha.

Similarly, if two cohorts of young females emigrate together from their natal pack, a relatively rare occurrence in Moremi Pack (McNutt 1996) a member of the oldest cohort become alpha (R. McNutt pers. comm.). Likewise in Serengeti (Scott 1991), sometimes mixed cohorts of females emigrated together but here the eventual dominant females were unknown. However, if a group of young females disperse with their mother she retains alpha status in any pack which they help to form (Frame et al 1979, R. McNutt pers. comm.). However in such cases when a new pack is formed then the young females can breed as subordinates as they like their mother will be unrelated to the new males. The mechanism(s) whereby the presence of their mother and/or father prevent oestrus in young female in their natal pack but allow the daughters to breed in their mothers new pack with unrelated males is unclear. Perhaps the absence of their father and male siblings is a factor.

Starter packs may be ephemeral due to the incompatibility of some single sex groups which meet. In Serengeti it was observed that a group of young males disrupted two resident packs one with an a single older female who they then left alone and later 'kidnapped' the 2 slightly younger females from another pack (Frame et al 1979, Frame & Frame 1986). In another case a group of young males interacted with a breeding lone pair pack but left them and joined a group of young females in an adjacent area to form a new pack (pers. obs.). In two other cases a lone male joined, then apparently left, a group of 5 young dispersing females and a lone male left an older lone female to join 2 new younger immigrant females (Scott 1991; pers. obs.). It appears from this limited series of observations and other published information that if 2 dispersing groups of young dogs (natal dispersers) of opposite sex each with an established dominant then it is more likely that a pack will form than if lone individuals of either sex, but particularly older females meet younger dispersing groups of the opposite sex.

An immediate problem for a newly established starter pack is that, as it usually consists of young relatively inexperienced members, they will have to attempt to carve out a sustainable year round home range in a 'foreign' habitat and may so come into conflict with existing larger Resident packs (see below) in that area and so suffer considerable harassment.

If it's members are successful in establishing a home range and the dominant pair raise pups (with the assistance of the other adults) once the pups become yearlings they will act as helpers to the dominant pair's next litter. However in its second year of existence secondary emigration of some or all of the alpha female's sisters will lead to a rapid decline in older adults and a male biased sex ratio (data in Frame et al 1979, Scott 1991).

Resident packs

Resident packs can be considered as 'Starter packs' that succeeded and flourished for a number of years. It will contain a number of cohorts of both sexes i.e. the dominant pair and any other same age relatives of either dominant, plus those born in the pack i.e. yearlings - perhaps older (c 24 months) and younger (c 12 months) plus new pups. Such packs can be large - 40+

In the Resident packs in Serengeti, following the death of one of the alpha pair the pack split into single sex adult groups one of which retains responsibility for any pups present. In Serengeti in the 1970s the males remained on their former packs home range with the pups any females of which subsequently emigrated when yearling. However, in Woodland Packs such as Moremi where packs occupy scent marked territories, as opposed to an ill defined vast home ranges of 1,500-2,000 km² as in Serengeti, either sex may remain on the original territory following the break up of the pack into single sex groups (said to be when the last founder member of either sex dies/leaves).

The other single sex group looked for new partners in areas adjacent to their former packs territories or disrupted existing resident packs from which they evicted same sex adults who sometimes took any pups present with them (McNutt 1996, McNutt & Boggs 1996, J McNutt per comm.).

In Serengeti the all male group resulting from the death of either dominant (c.f. stated cause of Pack Dissolution used by McNutt 1996), often of a number of cohorts, remained in the former packs home range. Here the males continued to bring up any pups of both sexes from the pack's last litter whilst awaiting the arrival of an immigrant group of females to re establish a pack. This 'wait' was sometimes a few days, weeks, months, or sometimes up to 2 years. These groups can thus temporarily 'lie fallow' during periods of low reproductive success in a population as in Serengeti in the 1970s (Frame et al 1979).

However, once the new females arrive a male from the youngest cohort present immediately emerged as the new alpha. His father, if he has survived, and any older males became highly subordinate but essential 'elders' in the pack. The new females in the pack adopted any pups present in the adult male group that they join. These pups on reaching 12 months acted as extra helpers to the pack's new alpha pair. The Serengeti *Lycaon* population could thus suddenly and dramatically expand given favourable ecological conditions as occurred post 1979 in Serengeti (Burrows et al 1994, Burrows 1995).

In Serengeti (c.f. Moremi) residency of a male group from the founder Resident pack continued despite the death over the years of either of the alpha pair. Such long term occupation of the limited number of 'most desirable' home ranges in the Serengeti plains habitat was vital to the survival of this *Lycaon* population which denned in the wet season (c.f. dry season in woodland habitat). Reproductive success was dependent on the proximity of the rainfall to the denning sites as was therefore the presence in its vicinity of vast migrant herds of herbivores in their turn so dependent upon rainfall and the new nutritious grass and locally available water for their successful reproductive season .

Sex ratio and pack size

Both will be entirely determined by the initial composition of the two single sex groups that meet to form a Starter pack or reconstitute a Resident Pack following pack dissolution.

Resident Pack longevity

If any male pups are present when the original pack splits, then on maturity (13m+), one of these will take over the alpha status from his older brother without overt aggression. The new alpha can, like his deposed elder brother, mate with the current alpha female (step-mother) to which none of the males are related. The first litter sired by the new young alpha pair will accept them as pack leaders so long as both are still present in the pack. Hence the pack can potentially continue as a breeding unit on their home range through the male line over many years

Most of the packs studied in the Serengeti between 1965-91 could be considered Resident with continuity of occupation of a home range for periods of up to 10 years through the male line. The older males (up to 12 years old) in the male group acted as repositories of essential information for the groups survival.

The cultural information the open savannah pack members 'inherit' from the older males would include the geography of the home range, such as areas of woodland, dense bush, or riverine forest which should be avoided, as all are areas where lion and leopard ambush is highly likely.

In woodland, unlike open savannah, lions are the major 'natural' cause of mortality of adults and pups. It is often claimed that Serengeti packs were subjected to high levels of predation of both adults and pups by lions and spotted hyaena.

It has even been claimed that predation by lions in Serengeti is at the same high rate as in the Kruger National Park. It is also stated that Serengeti wild dogs have to compete with lions and hyaena for water, and den sites as well as for the same prey. (S.Creel in Morell 1996). Such claims are false and have no scientific basis but often repeated in popular articles.

Other vital information passed on by the older males would include dry season water supplies, prey concentrations and the ranges of other packs with adjacent or overlapping home ranges. All such information held and transmitted through the male lineage would aid the long-term survival of the former Serengeti plains Resident packs.

For dispersing groups of young females an all-male group resident on a desirable home range would be an attractive proposition particularly for the alpha female in the group whose partner would be from the youngest cohort present. This union of young adults provides at least the possibility of a long and successful breeding life for the new alpha pair and hence the survival of the pack.

The basis for the persistence of a Resident pack is thus a group of related males of various ages from (<1-12 years old) which remain resident on a home range following the death of either of the current alpha pair.

This persistent male group, whose composition will naturally change over time due to death and recruitment, will be joined periodically by new groups of immigrant females, either from a local pack or who may have travelled a considerable distance (see data for 'Genghis Pack' in Frame et al 1979).

Sex Ratio in Resident Packs and varying fortunes of the Serengeti Resident study packs over time

As with the Starter Pack the Resident adult pack size will depend on the initial numbers of each sex but within a few months this will increase as any pups present reach yearling status (at 12 months). However the initial or primary sex ratio in a Resident pack is likely to be male biased. This is because a Resident pack when it is re-formed following the death of one of the alpha pair usually contains adult males from a number of cohorts often including one or more former alpha males and their brothers or other relatives. Hence the sex ratio in a Resident pack is more likely to be skewed to males.

The skew to males increases over the years as sisters of the alpha female secondarily emigrate until, of the initial group which joined the males, only the alpha female remains. The skew will also increase if reproductive success is only sporadic in the pack with some males born in the pack being recruited permanently into the pack in some years following poor pup survival.

This was the case in Serengeti in the plains packs of the late 1960s and during the 1970s (Malcolm 1979, Burrows 1995). If no male pups survived in their natal pack in any one year then one of the yearling males might have the chance to take over the alpha position if either of the alpha dogs died before new pups were produced. It is probably for this reason that young males delay their emigration until they have confirmed, probably via genital licking, that younger male pups have survived. By contrast yearling females in Serengeti packs had no chance of reproducing in their natal pack and all emigrated when between 15 and 24 months old.

Reproductive success in Serengeti study packs in the 1970s was very low and showed no correlation with the number of older adult helpers present (Malcolm 1979). Given the lack of immigrant groups of either sex entering the plains in the 1970s low pup survival affected packs over a wide area including the Masai Mara in Kenya. This suggests that the problem was disease related and probably canine distemper as it affected mainly pups and other younger dogs (Schaller 1972, Frame et al 1979).

There is therefore no need to invoke decline in mean adult pack size or kleptoparasitism and predation resulting from the increasing number of lions and spotted hyaena on the Serengeti plains in the 1970s as the cause of the observed decline in the *Lycaon* population.

There was no decline in the number of Resident packs which should be the basic unit of measurement of a *Lycaon* population. The evidence suggests that high disease induced pup/whole litter mortality led to a decline in mean adult pack size which affected the *Lycaon* over a wide area regardless of any changes in the local population density of lions and hyaena in Serengeti (Burrows et al. 1994).

As a result mainly of age related mortality of one of the alpha pair, all male groups resident on a home range were frequently formed in the 1970s. Any young females dispersing from the few plains packs which did raise pups to yearling status were thus able to join all male groups on home ranges overlapping, or a very short distance from, their natal packs home range. By contrast any dispersing male groups had to leave the area or attempt to steal females from existing packs -see below- (Frame et al 1979).

All changed post 1979 in Serengeti and the adjacent Masai Mara area and presumably over a much larger area given the number of unknown immigrants, with each year most packs successfully producing a litter of

pups. Consequently the older yearlings (mainly >18 mo.) of both sexes emigrated in single sex groups (primary emigration) with the females leaving before the males.

The departure of the older yearlings just before the new seasons pups were born dramatically reduced the number of experienced adults in the Serengeti packs. This left the younger yearlings (i.e. last seasons pups) to act as helpers to the next litter. If, as it is claimed, yearlings should be classified as 'dependants' (Creel & Creel 1995), and the presence of a number of older adults is critical to pup/pack survival, reproductive success should be correlated with the presence of the number of older adults(>2 yr.) present.

However in Serengeti between 1979-91 reproductive success (as measured by the number of pups surviving to >12 mo.), was not correlated with the number of older adults in the packs but with the number of yearling helpers (Burrows 1995). Thus post 1979 emigration of yearlings (18-24 mo.) was an annual event and the number of Serengeti packs and individuals was increasing up to early 1991 despite the increase in hyaena and lion populations and the sporadic catastrophic loss of whole packs from rabies (Fuller et al 1992, Burrows 1995, Burrows et al 1995).

It was not due to variations in pack size, kleptoparasitism by spotted hyaena or lion predation that all the study packs, but not the entire *Lycaon* population (contra Woodroffe & Ginsberg 1999) became extinct in both the Serengeti and the 'Mara' sectors of the Serengeti-Mara ecosystem between 1985-91. It was probably rabies in all cases (Burrows 1992, Woodroffe et al 1997, Burrows et al. 1994).

Male 'take over' of females from 'Resident packs'

In the Serengeti study there is one instance in which a group of dispersing males disrupted two existing small packs, both without pups, and 'kidnapped' 2 females from one pack and probably caused the death of at least one older male in the other. There were very few dispersing female groups from resident packs at this time no immigrant female groups and so females were in very short supply (Frame et al 1979).

By contrast there appear to be a large number of itinerant male groups and single males in woodland populations (McNutt 1996a). Such groups, as in the Serengeti example, may violently attempt to take over an existing pack in which a female(s) has male pups. This may be a possible explanation for the aggression reported at breeding time amongst males in Kruger (Mills 1993 and see below).

Female 'take over' of the males in a 'Resident pack'

A large male group in a Resident pack with a good home range would be an attractive group for itinerant young females to attempt to join, compared with a small group of land-less dispersing males. There is nothing in the Serengeti protocols, which might be expected to preclude such a take over.

It has been reported that groups of transient females in woodlands take over an existing pack by evicting resident females (Creel & Creel 1995).

In Serengeti young females sometimes joined existing packs (Frame et al 1979, Scott 1991). In 1990 two young unknown females (about 2 years old) joined a Serengeti 'Starter pack' consisting of a single 3 year old breeding female with pups and five 2 year old males. After some weeks the dominant young female attempted to take over the alpha role. This failed following a violent fight with the breeding female in which both combatants were extensively bitten (Burrows 1993, Burrows 1995).

In the failed female 'coup' the males in the 'Starter pack' did not attempt either to drive out the intruding females or to defend their existing breeding female (who was their aunt) from such a take over. In this case the alpha male would have retained his position at least temporarily as the males in the litter were new born.

In 'Resident packs' such a take over would be to the immediate advantage of any young males present as one would take over alpha status from his father and mate with one of the new females, his same age brothers having already accepted him as group leader. The apparent failure of young males in a 'Resident pack' to rally to defend their mother's position when young females try to take over isn't perhaps surprising.

The alpha female deposed following a coup would emigrate and could join a new group of males with or without any female offspring and still retain her alpha status. Genetically the former alpha female also gains in that she will usually leave behind a young son as alpha male in a 'Resident pack'.

Do the same protocols apply in southern African *Lycaon* Packs in Woodland habitats?

i. Does the all male group from a 'Resident pack' remain in their natal home range?

There is evidence that they do. In Moremi GR (Botswana) some males remained in their natal home range in woodland after the loss of the breeding female and were then joined by unrelated females (McNutt 1996b).

In the Selous GR (southern Tanzania) old *Lycaon* males often lost their rank to 'prime-aged-males' with many packs including one or more former alpha males (Creel & Creel 2002).

The presence of more than one former alpha male, (but with no former alpha females being mentioned) and the fact that older males do not emigrate suggests that in woodland packs, as in the Serengeti plains packs, all male groups remain in their packs former home range following the death of the alpha female.

ii. Does a young male take the alpha position in the all male group?

The answer to this question is currently unclear as not only is it necessary to know the natal pack of individuals in a study population but also their age before it can be confirmed that young males take over male groups. Such information is rarely reported or perhaps known. Even in the small number of closely monitored Serengeti packs mistakes were made in assigning alpha status to the older of the two males in two dispersing groups in the 1980s. This was based on the false assumption that older meant alpha (Scott 1991).

For example in the Moremi GR (see above) study population unfortunately it is not reported whether or not a young male remaining in its home range became alpha. However this must be a strong possibility otherwise the younger males might have been expected to emigrate. In the Selous GR the presence of a number of former alpha males in some packs would also suggest that the young male take over protocol applies in this population.

That the pack protocols based on Serengeti packs also apply to free living and captive packs is suggested by a wide variety of observations which would otherwise be very difficult to explain:-

i. The phenomenon of 'pack dissolution' and the formation of all male groups in free living populations after the death of an alpha individual in Kruger NP (Reich 1981).

ii. The take over of alpha status by a younger male who displaced his father in Kruger NP (Reich 1981)

iii. The presence of one or more former alpha males in many free living Selous packs (Creel & Creel 2002).

iv. Two younger hand reared males from Botswana became dominant over two wild bred (Kruger) older males, and one became alpha in a pack when the male group was joined by wild bred females in Madikwe GR in South Africa (Hofmeyr 2001).

v. The aggression in captivity following the introduction of adult males to an adult female with offspring. In six cases in southern Africa the young males (>4 months) consistently harassed the adult males. The reason for this behaviour is claimed to be not clearly understood (Hofmeyr 2001).

vi. In a captive pack in Mkomazi (Tanzania) aggression eventually resulted following the mixing of individuals of both sexes from different litters to form a single 'pack'. The problem emerged following the death of the alpha female which had a litter of pups. Her mate continued to look after the pups but lost his alpha position to an unrelated male. When the former alpha male's male pups became sub-adult, as in the southern African examples above, they hassled the new alpha male (Visee et al. 1998).

vii. In a captive colony in South Africa it is reported that a younger disabled male took the alpha position in a pack (van Heerden & Kuhn 1985).

The diverse and apparently unrelated, unexpected and unexplained events and behaviour described above can all be explained by the Serengeti 'young male first' protocol (Burrows 1995, Visee et al 2001).

The conclusion following from these observations is that in the wild the youngest male becomes alpha, and in captivity attempts to become alpha regardless of the genetic relationships between the males in a group.

What cannot be explained at present is the mechanism involved. Just how does an older male 'know' and passively (contra Creel & Creel 2002), in the wild, accept his changed status.?

It is conceivable that a small mutation some 2-3 MY ago in a canid ancestor of *Lycaon* in Eurasia caused a genetic 'switch' which, in the presence of pups, switches 'on' the behavioural imperative to adopt, feed and later to defer to pups at kills, to be left permanently 'on'. This could have occurred perhaps some 3 million years or so ago in Canid evolution resulting in a new Genus (*Lycaon*) living in extended families i.e. packs, with both pack formation and social hierarchies within it quite different from that of any other canid.

Some observations appear not to fit the concept of a stable male breeding hierarchy based on young male priority.

For example, in the *Lycaon* population in Kruger National Park another mainly woodland habitat, it is reported that an age related male hierarchy exists with older males dominated younger (Reich 1981) and :- "During the mating season competition between males for females may be severe particularly in packs with several adult males. During this time males may inflict severe injuries on each other ..." (Mills 1993) This would imply that in such cases, for some reason a male breeding hierarchy is either not present or poorly established. Unfortunately the frequency and circumstances surrounding aggressive male interactions in Kruger is again not reported.

The crowding of woodland packs near water in the dry season and the presence of dispersing groups of males due to low longevity of packs may contribute to intra specific male aggression in Kruger and possibly other wooded habitats. In Northern Selous another mainly woodland habitat it is suggested that intra-specific competition might have an appreciable effect in limiting *Lycaon* numbers in this high density population (Creel & Creel 1998).

More information about relationships of the individuals involved and their position in the social hierarchy is required before possible reasons for this aggression in woodland packs can be suggested.

Do sub-species of *Lycaon* exist?

Based on mtDNA analysis, it was originally claimed that two sub species of *Lycaon* existed. Now based on further such analysis it is claimed that there are merely two genotype clades which 'co-occur' over much of the present geographical range of the species (Girman et al 1993, Girman et al 2001).

Using similar mtDNA analysis to that used by Girman et al, it has been found that although three distinct species of northern European crossbill (*Loxia*) are currently recognised based on differences in beak shape, feeding techniques and the lack of interbreeding despite habitat overlap, they are genetically inseparable (Piertney et al 2001). However the authors caution that such genetic techniques must be used in conjunction with the more traditional methods of defining a species such as those based on behavioural and ecological studies. The same may be true of *Lycaon*.

Data from some woodland ecosystems show that the main social protocols identified in the Serengeti population also apply to other populations of *Lycaon*. Some apparent differences in patterns of dispersal and levels of aggressive behaviour, within and between packs, in woodland compared with plains packs may not be fundamental.

Differences could result from the relatively high population density of *Lycaon* and lions and hence higher levels of intra-specific and inter-specific aggression (mainly involving lions) leading to higher mortality in woodland, than in savannah packs. Death of one of the alpha pair and the frequent dissolution of woodland packs is perhaps the 'price paid' by *Lycaon* for denning near limited water supplies in the dry season.

Referring to the much studied Kruger Woodland *Lycaon* population it is claimed that: -

" In this species flexibility in social systems appears to be limited and the basic principles enumerated here are applicable to most wild dog populations". (Mills 1993) and :-

"...it seems unlikely that genetic differences between regions reflect extreme adaptation to unique ecological conditions" (Woodroffe & Ginsberg 1999).

If Mills (1993), Girman et al (2001), Woodroffe & Ginsberg (1999) are correct and there is no genetic evidence for either sub-species of *Lycaon* or genetically determined behavioural differences between populations, then it would be surprising if the Serengeti social protocols (relating to male breeding hierarchy and leadership) do not also apply to southern African woodland packs and packs in other habitats in Africa.

However, if there are important ecological and behavioural differences between open plains East African and southern African woodland *Lycaon* populations which do not manifest themselves in mtDNA analysis techniques currently used, the reliance on such evolving and uncertain techniques to guide conservation management of endangered species must be at least highly questioned.

The Serengeti 'youth first' and 'leadership' protocols has important implications for the management and conservation of *Lycaon* throughout Africa. This applies particularly to the increasing practise of translocations of individuals and groups and the handling of alpha individuals in packs. The risks involved in such activities should be fully taken into account by wildlife managers and those funding wildlife conservation when support for the undertaking and funding of such activities is requested.

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