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Crucial importance of pack size in the African wild dog *Lycaon pictus*

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Abstract

Although the massive organized slaughter of African wild dogs, *Lycaon pictus*, largely ended several decades ago, this endangered canid continues to decline and faces extinction. Several lines of evidence suggest that this arises from obligate cooperative breeding, which makes *Lycaon* more sensitive to anthropogenic mortality. A number of behaviours in this species are characterized by a reliance on helpers. These include cooperative hunting, defence from kleptoparasitism, pup feeding and baby-sitting. As a result, there are strong, positive relationships between pack size and the production and survival of pups, and pairs of wild dogs are often unsuccessful at raising offspring without the assistance of helpers. Consequently, a pack in which membership drops below a critical size may be caught in a positive feedback loop: poor reproduction and low survival further reduce pack size, culminating in failure of the whole pack. Here, we review the literature to reveal the importance of pack size in the African wild dog. Most importantly, we argue that there is a critical minimum threshold, below which packs face an increasing probability of extinction – an Allee effect with consequences for the conservation of this species, and of other obligate cooperators.

INTRODUCTION

African wild dogs, *Lycaon pictus*, also called painted hunting dogs (Rasmussen, 1999), have been consistently persecuted by human populations throughout known history (Estes & Goddard, 1967). Although the government-funded slaughter ended a few decades ago, anthropogenic mortality is still the main factor of African wild dog mortality (Fuller *et al*., 1992; Fanshawe *et al*., 1997). Remaining wild dog populations have shown dramatic decreases over the past 30 years, resulting in their disappearance from 25 of the 39 countries in which they were formerly recorded (Fanshawe *et al*., 1997). This has left the entire species with a much reduced geographical distribution and a small number of packs (600–1000, Fanshawe *et al*., 1997). Since most of the remaining populations number less than 100 individuals, it is predicted that, if nothing is done, extinction of the species could occur in the short term (Woodroffe & Ginsberg, 1997*a*). Averting this disaster requires understanding the causal mechanisms of the continuous decline of these populations. Here we focus on just one characteristic of the population dynamics of wild dogs, and attempt to link individual behaviour to population dynamics and thereby to explain an important element of their current decline.

It has been hypothesized that, because of their need for helpers, obligate cooperative breeders require a minimum size to persist as a group (Courchamp, Grenfell & Clutton-Brock, 1999*b*; Courchamp, Clutton-Brock & Grenfell, 2000). Theoretically, below this critical threshold, a social group that suffers what is called ‘inverse density dependence’ because of a lack of helpers will have a reduced survival and/or breeding success, which will further decrease its size, ultimately drawing it to extirpation. This is one form of Allee effect, an inverse density dependence at low density or population size, typically below a threshold (Courchamp, Clutton-Brock & Grenfell, 1999*b*; Stephens & Sutherland, 1999). Our purpose here is to review the literature to reveal the importance of pack size for African wild dogs.

Importance of pack size

African wild dogs live in packs of up to 20 adults and their dependent young (Childes, 1988; Fuller *et al*., 1992; Maddock & Mills, 1994; Creel & Creel, 1995). Generally, only the alpha pair breeds, assisted by several helpers who generally do not breed themselves. In Table 1 we summarize representative illustrations of the need for helpers in *Lycaon* for three aspects of their fitness: foraging, breeding and survival.

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Table 1. Mechanisms providing advantages to large packs in African wild dogs

	Advantage of large packs	Process	Examples of reference
Foraging	Hunting efficiency (lower energetic cost)	Simultaneous attacks	Fanshawe & FitzGibbon, 1993; Creel & Creel, 1995
		Prey isolation	Kühme, 1965; Creel & Creel, 1995
		Distract mother from calf	Fanshawe & FitzGibbon, 1993; Creel & Creel, 1995
		Intercept prey after shortcut	Kühme, 1965; Estes & Goddard, 1967; Creel & Creel, 1995
		Shorter chases	Creel & Creel, 1995
		Simultaneous kills	Creel & Creel, 1995
	Prey species range	Pull prey together to a halt	Creel & Creel, 1995
		Maintain/distract prey while being disembowelled	Fanshawe & FitzGibbon, 1993; Creel & Creel, 1995
	Injury reduction	Maintain head	Creel & Creel, 1995
	Prey killing	Coordinated tearing apart	Estes & Goddard, 1967; Carbone *et al*., 1997
	Carcass eating	Coordinated carcass opening and dismembering	Estes & Goddard, 1967; Rasmussen, unpublished data
	Defense from kleptoparasites	Rapid carcass cleaning	Estes & Goddard, 1967; Fanshawe & FitzGibbon, 1993; Rasmussen, unpublished data
		Intimidation by numbers	Malcolm & Marten, 1982; Fuller & Kat, 1990; Fanshawe & FitzGibbon, 1993; McNutt, 1996*a*
	Steals from kleptoparasites	Intimidation by numbers	Creel & Creel, 1995
Breeding	Litters size	Prior access to kills to breeding female and juvenile	Malcolm & Marten, 1982
		Pregnant/suckling female fed by regurgitation at the den	Malcolm & Marten, 1982
	Pup care	Facultative communal care	Kühme, 1965; Fuller *et al*., 1992; Burrows, 1995
		Pups fed by regurgitation for 3 months	Kühme, 1965; Malcolm, 1979; Malcolm & Marten, 1982
		Parts of a kill carried to pups	Malcolm & Marten, 1982
		Pups led to kills	Malcolm & Marten, 1982
		Pups given priority at kills	Malcolm & Marten, 1982
Survival	Pup survival	Baby-sitting (+ baby-sitter fed by regurgitation)	Kühme, 1965; Malcolm & Marten, 1982
		Pup defence against predators	Kühme, 1965; Malcolm & Marten, 1982; McNutt, 1996*a*
		Pup adoption	McNutt, 1996*a*
	Adult survival	Injured and older dogs tolerated at kills	Estes & Goddard, 1967; Malcolm & Marten, 1982
		Increased predator vigilance in large packs	McNutt, 1996*a*
	Intraspecific competition	Clashes between packs	Creel & Creel, 1995, 1998
	Larger dispersing cohorts	Lower mortality	Creel & Creel, 1995
		Possibility of pack takeover	Creel & Creel, 1995; Creel *et al*., 1998
		Better chances of successful establishment of new pack	Creel & Creel, 1995

Foraging

Lycaon helpers contribute to diverse aspects of foraging. Wild dogs are known to hunt cooperatively, typically in packs of between seven and ten (Schaller, 1972; Fanshawe & Fitzgibbon, 1993; Fuller & Kat, 1993; Creel & Creel, 1995). There is evidence that several individuals hunt more efficiently than do pairs or singletons (Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1995). Specifically, wild dogs cooperate to isolate prey, launch simultaneous attacks, intercept fleeing animals after a shortcut, distract mother from calf, together pull a prey to a halt and restrain it while being killed (Creel & Creel, 1995). Together with reducing the risks of injury from large or well-armed prey (Malcolm & Marten, 1982; Creel & Creel, 1995), hunting in larger packs extends the range of prey species that a pack can hunt – an advantage when smaller prey are not available close to the den during the denning period (Fanshawe & Fitzgibbon, 1993). Therefore, not only does hunting success (percentage of kills per hunt) increase with pack size, but so does the mass of the prey killed, while the distance chased per hunt decreases with pack size (Creel & Creel, 1995).

A second benefit of larger pack size to foraging for *Lycaon* concerns defence of the kill from kleptoparasites. Spotted hyaenas, *Crocuta crocuta*, and lions, *Panthera leo*, regularly steal the kills of wild dogs (Fanshawe & Fitzgibbon, 1993; McNutt, 1996*a*; Carbone, DuToit & Gordon, 1997; Gorman *et al*., 1998), sometimes even before the captured prey is killed (Estes & Goddard, 1967; Creel & Creel, 1996). A small loss of food to kleptoparasites may have a large impact on the amount of time that dogs must hunt to achieve energy balance (Gorman *et al*., 1998). Larger packs are able to retain kills from hyaenas for longer (Malcolm & Marten, 1982; Fuller & Kat, 1990; Fanshawe & Fitzgibbon, 1993; Creel & Creel, 1996; McNutt, 1996*a*; Carbone *et al*., 1997). *Lycaon* themselves engage in kleptoparasitism and have been documented stealing the kills of leopards, lions and hyaenas (Creel & Creel, 1995), and it seems likely that larger packs would be at an advantage in accomplishing such thefts.

Lycaon kill their prey by tearing it apart, dogs grabbing it from all sides and pulling against one another (Estes & Goddard, 1967; Carbone *et al*., 1997). This task, together with dismembering the carcass, is more rapidly accomplished by many dogs than by few, decreasing the time for which the kill is available to kleptoparasites. Wild dog digestive tracts are exceptionally adapted to allow rapid ingestion of large amounts of meat, and to regurgitate these later on (Ewer, 1973: see below). Each dog can carry 3 days' worth of food, a full stomach containing up to 4.4 kg of meat (Reich, 1981 in McNutt, 1996*a*), and possibly twice that amount (Creel & Creel, 1995). Rapid consumption and successful defence of a kill reduces the number of hunts necessary, and consequently their energetic cost (Gorman *et al*., 1998) as well as the risks linked to the hunt (accident, predator encounter, death of the pups left behind, Malcolm & Marten, 1982; Creel & Creel, 1995). Smaller packs are slower to dismember and eat carcasses, but also may be unable to consume all the flesh and obliged to leave food behind, thereby promoting the survival of competitors.

Breeding

Cooperation is crucial to *Lycaon* pup-rearing. Their litters are uniquely large amongst canids: averaging 10–11 pups, maximum 21 pups (Fuller *et al*., 1992). In general, only the alpha female bears and nurses pups. When a subordinate female breeds, the alpha may simply take her pups and suckle alone the combined litters (Burrows, 1995), but more commonly the females share the burden of suckling the two litters in a communal den (Kühme, 1965; Fuller *et al*., 1992; Burrows, 1995). In addition to providing alternative rest periods to the two mothers (who may participate in hunts sooner, Malcolm & Marten, 1982), this may also have a survival value for the two litters, since it may allow the transfer of more maternal antibodies to both of them (Roulin & Heeb, 1999).

In the context of the Allee effect, a more important aspect of cooperative breeding lies in *Lycaon*'s regurgitating behaviour. African wild dogs are able to ingest and then regurgitate large amounts of meat, on average about 1 kg of meat after a full meal (Kühme, 1965; Ewer, 1973; Malcolm, 1979, in Fuller & Kat, 1990). In this way, they may feed the pregnant mother, whose ability to hunt is compromised in late pregnancy and early lactation (Woodroffe & Ginsberg, 1997*a*). They also feed the pups for 2 to 3 months by regurgitating meat (Estes & Goddard, 1967; Malcolm & Marten, 1982), even if the mother dies before their independence (Estes & Goddard, 1967; McNutt, 1996*a*). Pack members also give pups priority access to food, even when it is scarce, although, when very hungry, juveniles may not regurgitate to the pups (Malcolm & Marten, 1982). As the pups mature, some adults may carry part of a kill to the pups for them to chew (Malcolm & Marten, 1982). Later still, the pups follow the adults to the kill (or are led there by juveniles), where they will again have the possibility of feeding first while the adults guard the carcass (Malcolm & Marten, 1982; Rasmussen, 1997).

This helping behaviour may facilitate large litter sizes. Certainly, litter size is correlated with pack size (Vucetich & Creel, 1999). Although limited by small sample size (packs of five or less were rare and seldom bred successfully), other published data are suggestive of this effect (Fuller *et al*., 1992).

Survival

A third point where the cooperative behaviour of wild dogs is of major importance concerns survival, for example during interactions with natural enemies. Breeding females can regain hunting condition 3 weeks after parturition. Her return to the hunt is important, especially as alpha females often lead hunts (J. McNutt, pers. comm.; G. Rasmussen, pers. comm.). However, litters cannot follow the pack for another 2 months. A baby-sitter may then be left with the pups while the rest of the pack is hunting. The baby-sitter must chase away predators, make sure the pups do not stray, and warn them to go down the den if danger threatens (Kühme, 1965; Malcolm & Marten, 1982). However, leaving a baby-sitter behind is costly for three reasons. First, this individual will have to be fed by meat regurgitated from the hunting party, thereby diminishing the food available for the pups (Kühme, 1965; Malcolm & Marten, 1982). Second, the baby-sitter's absence lowers the hunting efficiency of the pack (which is related to the number of hunters). Third, it also reduces by 4 kg or so the food brought back to the den (plus that food then becomes available to competitors). In fact, the threshold pack size at which leaving baby-sitters on duty becomes generally economic seems to be around five individuals (Courchamp *et al*., in press).

African wild dogs do not take risks to defend a carcass from lions or hyaenas, but will aggressively mob potential predators if these threaten the pups (e.g. Kühme, 1965; Estes & Goddard, 1967). The ferocity and organization of their defence can drive off spotted hyaenas, jackals, leopards or even lions (Malcolm & Marten, 1982; Creel & Creel, 1995; McNutt, 1996*a*), an important cause of mortality in wild dogs (Mills & Gorman, 1997). Large packs are evidently more efficient at mobbing predators than are intermediate sized packs.

In addition, incapacitated individuals (because of a debilitating disease or injury) are tolerated at kills by other members of the pack even when they cannot participate in the hunt (Estes & Goddard, 1967), and may be fed by regurgitation (G. Rasmussen, unpublished data). Clearly, this is likely to enhance the chance of recovery and subsequent full participation in the pack. Older members, less able to hunt, may none the less efficiently chase predators from the dens, and regurgitate generous amounts to the pups, and are tolerated at kills (Malcolm & Marten, 1982).

Consequences at the pack level: direct empirical evidence

Although the weight of literature strongly suggests an Allee effect in *Lycaon*, proof is elusive. Each of the three fitness components reviewed above seems positively linked with pack size, but none can be unequivocally proven individually. However, one of the most straightforward ways of evaluating the importance of pack size for wild dogs is to compare the number of pups successfully raised to independence for different pack sizes. Any such relationship can be attributed to a combination of an improved foraging efficiency, breeding success and survivorship in larger packs. Analysis of empirical data showed in several studies that the number of pups successfully raised increases with pack size (Malcolm & Marten, 1982; Burrows, 1995; Creel, Creel & Monfort, 1998; G. Rasmussen, unpublished data).

Consequences at the population level

Intraspecific competition has been implicated as a major cause of adult and pup mortality (Creel & Creel, 1998). An encounter between two packs may result in severe fights leading to lethal injuries: in Selous, seven wild dogs were killed in such inter-pack fights (Creel & Creel, 1998). In these clashes, the larger pack always took the advantage over the smaller one (ten cases, Creel & Creel, 1995). In absence of other selective pressure acting in the opposite direction, this could be sufficient for a natural selection towards larger groups to occur.

Wild dog pack dynamics are also influenced by dispersal of young adults. Generally, several males of the same cohort disperse together, and may join lone females, or a cohort of females (Frame *et al.*, 1979; Fuller *et al.*, 1992; Burrows, 1995; McNutt, 1996*b*). Mortality during dispersal is likely to be important, considering the large distances and dangers involved. Large packs are more likely to produce large sex-same dispersal cohorts, which may lower the mortality during dispersal (Frame *et al.*, 1979; Creel & Creel, 1995). Smaller packs may not produce dispersers, or produce too small a cohort for it to survive long enough to establish itself on an empty territory. In addition, the fewer (and the smaller) the neighbouring packs, the less single-sex cohorts of the opposite sex are potentially available, which may increase the time before mate location and new pack establishment (Frame *et al.*, 1979). Finally, because of a probable pack size threshold, the union of two small dispersal units (of one or two dogs) is less likely to produce a successful new pack than if two larger units join. All this has been shown to occur with a theoretical model (Courchamp *et al.*, 2000). This is supported by empirical data from Selous and Serengeti, where pack extinction rates of 16% to 37% per year have been recorded between 1985 and 1991 (Burrows, 1995; S. Creel, unpublished data, see also Ginsberg, Mace & Albon, 1995).

DISCUSSION

Our synthesis reveals many aspects of *Lycaon* behaviour – including foraging, breeding and survival – for which a critical number of members is essential for the persistence of packs and populations. It may be important to note that we do not imply that African wild dogs cannot reproduce below this critical pack size: there are some anecdotes of that. Our point is rather that statistically the break point between success and failure hovers around a pack size of five adults.

Our aim is to emphasize an additional force for the extinction and decline of wild dogs throughout Africa that aggravates disproportionately the widely acknowledged dangers threatening this species. We argue that the impacts of the probable causes of these population declines – persecution, habitat destruction and natural enemies (predators, competitors and parasites) – are magnified by the very nature of the dynamics of obligate cooperative breeders. This concept has not been advanced as a potential cause for high rate of pack extinction, although the importance of pack size has previously been emphasized by wild dog specialists (Estes & Goddard, 1967; Malcolm & Marten, 1982; Fanshawe & Fitzgibbon, 1993; Fuller & Kat, 1993; Burrows, 1995; Creel & Creel, 1995; McNutt, 1996*a*; Carbone *et al.*, 1997; Creel *et al.*, 1998; Vucetich & Creel, 1999).

Obviously, there will be upper limits to group size through intra-group competition, for feeding and for breeding opportunities, and ultimately because of a diminished marginal advantage of expanded membership (Macdonald & Carr, 1989). The existence of such an optimum should be expressed as a dome-shaped distribution of pack size, explicable if populations were subject to an Allee effect: inverse density dependence at low density and direct density dependence at high density (in this case it is pack size, rather than density, which matters). This is exactly the type of distribution, with a mode at ten dogs, observed in the largest existing population of African wild dogs: Selous Game Reserve in Tanzania (Creel, 1997). Literature data reanalysed by Fuller and co-authors (1992), as well as studies from Childes (1988) and from Maddock & Mills (1994), confirm this average pack size at ten adults. Irrespective of the precise values or the minimum threshold and optimum pack size, it appears that these two crucial numbers are not widely separate, which suggests that a delicate balance exists, from which *Lycaon* may readily be perturbed.

From a conservation perspective, the existence of a critical pack size for wild dogs implies two different options for wild dog conservation. Obviously, pack sizes should not be eroded towards the critical threshold, which requires alleviating the major causes of individual mortality: persecution and human activities (e.g., snare poaching, road traffic and domestic dog induced epidemics) (Maddock & Mills, 1994; Woodroffe & Ginsberg, 1997*a*). Wild dog conservationists have long advocated such approaches. A less obvious line of thought would be to increase artificially the size of packs known to be at risk because of low numbers. While release of captive-bred *Lycaon* has proven problematic (Scheepers & Venzke, 1995), wild dogs readily accept unrelated individuals, or even adopt unrelated pups or juveniles (McNutt, 1996*a*). In this regard, the fact that all four documented cases of adoption of unrelated pups came from 'smaller-than-average groups' (McNutt, 1996*a*) may be considered as a further indication that pack size *per se* is a major factor influencing wild dog survival. Artificial constitution of packs in captivity also shows some promise (Rasmussen, 1997; Woodroffe & Ginsberg, 1997*b*; Woodroffe & Ginsberg, 1999). At the least, the concept of critical threshold should be considered when planning wild dog translocations. In this context, it is noteworthy that the number of packs is also of critical importance for a closed population to persist (Courchamp *et al*., 2000).

Our critical analysis of the literature has revealed compelling evidence of a threatening Allee effect for *Lycaon*. Other highly cooperative species are likely to be equally susceptible to these processes, making it a priority to test empirically the largely theoretical evidence that the operation of this process at the group level will create an additional Allee effect at the population level.

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