Do dholes (*Cuon alpinus*) live in packs in response to competition with or predation by large cats?

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Interactions between carnivores during the defence of kills may be one reason why certain carnivores live in groups. This is especially true of lions, hyaenas and the African wild dog. The dhole or the Asiatic wild dog, primarily a pack living animal, has been observed to regularly interact with both tigers and leopards. Such interactions have taken place over kills and otherwise. In this report, five such interactions are described. It was found that the pack's behaviour of surrounding bushes and trees on which the cat was confined precluded immediate escape. The presence of sentinels, while the pack was resting, warned the pack of the presence of a big cat and the pack grouped when a big cat appeared. Costs to both individuals within the dhole packs and the cats involved in the encounters were found to be slight. The reasons for such potentially costly encounters could be competition for finite food resources or thwarting predation. Dholes have a significant diet overlap with both leopards and tigers and aggressively encounter with leopards but not with tigers. Differences between diet overlaps may not be the basis behind the differences in aggression. It is more likely that, the small size of leopards and the fact that they predate more often on dholes, cause dhole packs to be more aggressive to leopards than to tigers. The size of carnivore groups may thus pose an advantage during competitive interactions among carnivore species.

Agonistic interactions between carnivore species have been observed during the defence of kills. Lions (*Panthera leo*) regularly defend their kills from the spotted hyaena (*Crocuta crocuta*)[1]. One of the adaptive forces moulding the formation of packs in the African wild dog (*Lycaon pictus*) may be the advantage in numbers for the defence of kills from other species such as the spotted hyaena and for appropriation of kills from other carnivores. In the Selous National Park, Tanzania, wild dogs co-operated in the defence of kills from spotted hyaenas which managed to appropriate only 2% of wild dog kills (Creel and Creel, unpublished manuscript). In contrast, in the Serengeti National Park where hyaenas live in larger groups, the duration that wild dogs retained their kills depended on the ratio of individuals of the two species present[2]. Selous wild dogs often appropriated kills from other carnivores. Very pertinent to this report were the observations that leopards were driven up trees on two occasions and on one of these occasions a kill was appropriated (Creel and Creel, unpublished manuscript). Hyaenas and lions were also occasionally driven off kills which were later appropriated (Creel and Creel, unpublished manuscript).

Accounts of interactions between dhole or Asiatic wild dog packs (*Cuon alpinus*) (for a description of dhole biology, see refs. 3 and 4) and other major carnivore species do occur, with most of the accounts concerning those with the tiger (*Panthera tigris*) and the leopard (*Panthera pardus*)[3,5–13]. The outcome of these encounters though more often favouring the dhole packs involved (when tigers or leopards were killed or driven off), did on occasions result in members of dhole packs getting wounded or killed.

Here I report five separate instances of a dhole pack interacting with four leopards and one tiger (Table 1). One encounter involved one of our study packs and four, the other. The two dhole packs involved in the encounters have been monitored since 1988 and have their home ranges within the Dr J. Jayalalitha sanctuary (formerly Mudumalai sanctuary), Nilgiris District, Tamil Nadu, India[4]. Corroborating the above observed encounters are three other encounters (dhole packs interacting with two leopards and one tiger) which have been reported to the author by other observers. Based on this evidence I feel that such encounters are at the least, not infrequent and have a strong basis behind them. This paper therefore describes the above five encounters and attempts to look at two hypotheses as to why such encounters take place. The first hypothesis is that dhole packs aggressively encounter with leopards and prefer not to with tigers, as the former's prey may significantly overlap with that of dholes while the latter's does not. Coupled with overlap in prey are the relative differences in body weights between the two cats in question and a pack of dholes. Leopards weigh 2–3 times less than tigers do and are an easier adversary for dholes to take on[14]. Even if tigers' prey overlap significantly with those of dholes, the greater body weight differences may result in a high cost of interaction causing the interacting dhole pack to avoid tigers. The second hypothesis is that leopards may prey on single dholes and the aggressive encounters occurring within common hunting areas may drive away leopards, at least temporarily, thwarting sneak attacks on single dholes separated from the pack while hunting.

Table 1 summarizes the details of the above encounters. In all cases where dhole packs encountered leopards, a considerable amount of effort was deliberately put into

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Table 1. Details of dhole–large cat interactions

Date	Cat	Estimated wt. of cat (kg)	No of adults	No. of pups ≤ 1 yr	Context	Behaviour of cat	Behaviour of pack	Time spent in interaction (min)	Consequence
21.8 93	Leopard	50	8	6	None	Climbed 4 separate trees	Entire pack surrounded all 4 trees on which cat climbed and initially prevented cat from climbing down	50	Leopard escaped without wounds or wounding any dhole
9.1 94	Leopard	80	5	1 (1 yr 1 month)	Den	Climbed bush	Entire pack surrounded bush on which cat climbed and prevented cat from climbing down	96	Leopard escaped without wounds, inflicted scratches on 2 dholes
23 5 94	Leopard	50	11	6	None	Climbed tree	Entire pack surrounded tree	20	Leopard escaped without wounds or wounding dholes
16 9.94	Tiger	> 200	10	8	None	Initially approached pack and then moved away	Single dhole gave alarm calls after seeing tiger. Single dhole confronted tiger and then moved away. Pack moved away and bunched up.	5	Mutual avoidance resulting in no wounds to tiger or dholes
18.1.95	Leopard	50	8	2	Chital kill	Leopard driven from its kill and then driven up tree	Dholes kept leopard up tree after hunting sambar unsuccessfully and consumed entire carcass	30	Leopard left after dholes finished eating carcass and left

harassing the carnivore. The encounter with the tiger suggests, in contrast to the literature, that dholes may prefer not to engage directly with a larger adversary. An earlier account, reported by an observer to the author, which occurred during the study period, confirmed this speculation. A pack of six animals was enough to engage a leopard for 1 h 35 min with a small cost to pack members. Ten dholes were sufficient to deter a tiger from confronting with the pack. Nine dholes could appropriate a kill from a leopard, after hunting unsuccessfully for at least the last 24 h, thereby providing an alternative source of food.

The first hypothesis tested is that such interactions arise over competition for finite food resources. Out of 12 species the three carnivores feed on[15], we have chosen 5 for subsequent analysis. The hair of 5 species have been identified in the scats of the three carnivores, collected from the study area (Arumugam, unpublished). Because of the lack of density estimates, data from black naped hair (*Lepus nigricollis*) has been deleted from any analysis involving density estimates. Observed values of the 4 prey species for each predator are the occurrences of hair of each prey species among the total scats collected from that predator. In a chi-square test for independence, expected values are obtained by assuming that hair occurs among scat in accordance to the number of scats produced from a kill of each prey species and the densities of the 4 prey species within the home ranges of the 2 study dhole packs[15]. From a 3×4 contingency table (Table 2), with the 4 prey species as rows and the three carnivores as columns, we obtain a chi-square value of 1158 (d.f. = 6, $P < 0.01$). All three carnivores kill far more chital and sambar than expected but less gaur and cattle which gives rise to the highly significant result. A niche overlap index was also calculated[16]. Black-naped hare and another class called 'others'[4] has been included in the analysis. The values obtained are dhole–leopard: 0.922, dhole–tiger: 0.915, leopard–tiger: 0.939. This analysis indicates that there is considerable over lap between the diets of each of the three carnivores and the overlap is similar for all carnivore pairs. Therefore, if prey overlap is the reason behind the dholes aggression towards carnivores, they should be equally aggressive to leopards and tigers.

The other hypothesis tested is that leopards may predate on single dholes and such encounters deter them from doing so, by driving them away, at least temporarily, from common hunting areas. Predation on dholes by leopards, though not observed during the study period (October 1990–March 1995), has been reported in the literature[11]. Dhole hair occurred in 2% of leopard scat (as compared to 0.6% of tiger scat)[15]. Dholes while resting, always have a sentinel and are alerted by alarm

Table 2. Observed and expected numbers of occurrences of hair of 4 prey species found in scat of dhole, leopard and tiger

Prey	Dhole Obs.	Dhole Exp	Leopard Obs	Leopard Exp	Tiger Obs	Tiger Exp
Chital (*Axis axis*)	501	280 93 (172 40)	117	80.45 (16 60)	43	29 45 (6.23)
Sambar (*Cervus unicolor*)	243	78 52 (344 54)	76	24 19 (110 93)	48	12 45 (101 53)
Cattle	136	347 30 (128 56)	82	110 93 (7.54)	19	40 43 (11 36)
Gaur (*Bos gaurus*)	0	173 25 (173 25)	1	60.42 (58.44)	1	28 67 (26 70)

Total chi-square value = 1158 09

Densities (in km^2): Chital = 25 03, Sambar = 6 61, Cattle = 23.39, Gaur = 14.38. Data from ref. 20.

Chi-square values for each cell entry, in brackets.

calls of other mammals such as the common langur (*Presbytis entellus*), chital (*Axis axis*) and sambar (*Cervus unicolor*) (Venkataraman, unpublished). Furthermore, in the second encounter described, the leopard was in the proximity of a den containing young pups. It is very likely that harassment may deter sneak attacks on single dholes and pups. Dholes often separate during hunting and have elaborate acoustic communication for reassembling[3]. As mentioned earlier, packs have vigilant members who may thus deter attacks on the group.

In the Bandipur National Park, Karnataka, India, leopards and dholes competed for similar-sized prey but competition was reduced by the leopard's ability to climb and cache prey in trees. Moreover dholes killed more fawns and aged chital, while leopards killed chital of all ages. Tigers may coexist with dholes because of several factors such as spatio-temporal use of habitat and sex and size of prey[17]. Leopards and dholes killed prey of the same weight class while tigers killed prey of a higher weight class. Dholes, however, had a preference for male chital, while leopards did not. Tiger predation was biased towards adult males in chital, sambar, wild pig and towards young gaur[15]. Even though a significant diet overlap has been reported in this paper, competition may be reduced by niche partitioning based on age and sex differences of the prey species and spatio-temporal use of the habitat and prey. This may still cause a reduction and consequent difference in the overlap between the diets of dholes, leopards and tigers. However it is more likely that because leopards are smaller in size and predate more frequently on dholes, they are more aggressively dealt with than tigers are. Even though the ultimate reasons for such confrontations cannot be elucidated with certainty, it is quite evident that a pack could successfully accomplish what a single dhole or even a pair may not. Pack members successfully kept leopards on trees and bushes by surrounding them. A pack could obtain food by driving a leopard away from its kill. A single dhole detected a tiger and warned the pack. The pack bunched up invoking ideas of the selfish herd paradigm[18]. The tiger did not directly confront the pack avoiding a major cost to the pack.

Speculations about the evolution of group size in carnivores have hitherto concentrated primarily on the benefits of numbers while hunting[19]. This report brings to light another advantage of numbers in geographical regions where conflicts between major carnivores may be a definite selective force for the evolution of groups.

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