J. Zool., Lond. (1995) **237**, 543–561

The foraging ecology of dhole (*Cuon alpinus*) in Mudumalai Sanctuary, southern India

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(*Accepted 15 September 1994*)

(With 3 figures in the text)

Two dhole (*Cuon alpinus*) packs were monitored in Mudumalai Sanctuary, southern India, during 1989–93 to look at population dynamics, movement pattern, and foraging strategy and their inter-relationship with the maintenance of social groups. Pack size fluctuated substantially (4–18 and 4–25 in the two packs) owing to dispersal and demographic factors such as females not breeding in a given year. Both packs killed a much higher proportion of chital (*Axis axis*) and sambar (*Cervus unicolor*) fawns (< one year old) than their availability in the population. There was no correlation between pack size and body weight of prey killed, while per capita consumption of meat declined with increasing pack size. Home-range area (83·3 km^2 and 54·2 km^2 for the two packs) was not correlated with pack size. Pack movement from one resource patch (consisting of resting sites and aggregations of prey species) to another was not random or based on factors such as inter-patch distance or relative prey densities. There was no difference in mean residence time of the pack across the four resource patches; the pack moved across these in a sequential manner in one direction. We conclude that dholes live in groups not because of any advantages accruing from enhanced group sizes through increased per capita yield of food, but as a consequence of the dispersion of resources.

Contents

Introduction

Studies on the interactions between social carnivores and their prey species have resulted in useful insights into the evolution of group formation, cooperative hunting, and optimal foraging (Caraco & Wolf, 1975; Kruuk, 1972, 1975; Giraldeau, 1988; Giraldeau & Gillis, 1988; see Packer & Ruttan, 1988 for a review). Such studies often involve an examination of correlations between grouping patterns and hunting success. In lions (*Panthera leo*), increased hunting success is found to be an insufficient explanation for the formation of groups (Caraco & Wolf, 1975; Packer, 1986; Packer, Scheel & Pusey, 1990). On the other hand, for the African hunting dog (*Lycaon pictus*) success of hunting wildebeest (*Connochaetes taurinus*) was found to be positively correlated with

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group size. Furthermore, hunting in larger groups reduced interspecific competition from spotted hyenas (*Crocuta crocuta*) (Fanshawe & Fitzgibbon, 1993).

Apart from enhanced hunting success, other ecological determinants may influence the evolution of the optimal group size and foraging strategies. Dynamic models provide a method whereby different combinations of group sizes and foraging strategies may result in different survivorships of group individuals and hence genetic fitness (Houston *et al.*, 1988). These models attempt to incorporate information on both an animal's group life and foraging ecology. It has been used, for instance, to provide support to Packer's (1986) hypothesis that, under ecological conditions similar to the African savanna, conspecific scavenging within lion prides is highly advantageous to individual lions and may have fostered the evolution of sociality in the species.

Yet another theoretical paradigm which explores the influence of an animal's foraging ecology on its social life is the Resource Dispersion Hypothesis (Macdonald, 1983). In brief, this hypothesis provides an explanation for the addition of individuals to the basic unit of a breeding pair. Such additions are governed by the patterns of resource dispersion, where resources may be prey, mates, breeding sites, etc. Other selective pressures, such as the benefits of strength in numbers for defence of kills and territory, not to mention hunting and killing of larger prey, may operate within constraints set by patterns of resource dispersion.

The Asiatic wild dog or dhole (*Cuon alpinus*) is a highly social canid and a vigorous pack hunter whose distribution encompasses much of South-east Asia (Pocock, 1936; Johnsingh, 1982). It is a carnivore whose cooperative hunting strategies may be influenced by the behaviour, demography, and distribution of the prey species. In this paper, we look at the foraging strategy of two packs of dholes laying emphasis on how they utilize the principal prey species. Basic ecological data such as pack dynamics, home-range sizes, movement patterns, and prey selection by dholes are first reported. A pack's movement pattern is then analysed to arrive at a plausible strategy of how this pack utilizes its prey species. An explanation for how this strategy may account for certain observed aspects of its social biology is finally provided.

Methods

The study area

The study was carried out in Mudumalai Wildlife Sanctuary (321 km^2 area, 11° 32′ to 11° 43′ N latitude, 76° 22′ to 76° 45′ E longitude) at a general altitude of 800–1200 m above msl in the Tamilnadu state of southern India. A distinct rainfall gradient extends from the south and west (higher rainfall) to the north and east (lower rainfall) with corresponding changes in vegetation from tropical moist deciduous forest through dry deciduous forest to dry thorn forest (Sukumar *et al.*, 1992). Mudumalai is part of a much larger natural ecological unit in the Nilgiri Biosphere Reserve, comprising Bandipur and Nagarhole National Parks to the north, Wyanad Sanctuary to the west, and the Sigur Reserve Forest to the east. Descriptions of the flora and fauna of this region are available in Nair *et al.* (1978) and Karanth & Sunquist (1992).

The study packs

Two packs of dholes in the sanctuary were monitored for changes in pack size caused by immigrations, emigrations/deaths and additions from new litters during the period 1989–1993. The 2 packs are termed as the Kargudi pack and the Masinagudi pack (the villages of Kargudi and Masinagudi being the approximate centres of their home ranges).

Dholes older than 2 years were usually distinguishable. Such animals were identified from coat colour variations, nicks in the ears, ear folding, and prominent bone protuberances on the forehead. In total, 8 adult individuals from the Kargudi pack and 6 from the Masinagudi pack were identified during the study period. Pack identities were based on recognizing these individuals. It was seen that packs were cohesive entities. Pack members separated only when animals leading hunts left remaining pack members behind. The packs usually reassembled within 30 min of the hunt.

Other packs' home ranges lay adjacent to those of the 2 study packs. Apart from a small degree of overlap at the boundary, incursions by neighbouring packs into the home ranges of the study packs were rare and recognizable. From our surveys over a larger area, we believe that 5–6 packs inhabit Mudumalai Sanctuary.

Monitoring of pack numbers, movement and home range

The method of following the packs was as follows. The observer would set out for the field in the morning for a site where a dhole pack had either been sighted or had left indirect evidence the previous day. If the pack was located it was followed as long as possible for that day (which sometimes may have been the entire day). The locations at which the dholes were initially sighted, at which they were last seen during the day, and at which they were seen at the farthest distance from the location of the first sighting, were plotted on a 1:50,000 scale topographical map of the area.

Home-range analyses were carried out using McPaal Version 1.2 (McPaal, 1985). This involved fitting a minimum convex polygon to the location data (Mohr, 1947; Jennrich & Turner, 1969). We performed the analysis for data sets corresponding to all location data obtained during the period April 1990–December 1992. The Kargudi pack was located on 276 days and the Masinagudi pack on 103 days during this period. Location data obtained for the dry seasons (December 1–April 31) and for the wet seasons (May 1–November 31) were analysed separately. Location data obtained for different pack sizes were also analysed. For this, data obtained during the period April 1–November 31 were used. During the period December 1–March 31, dhole pups are incapable of freely moving with the pack which is more or less confined to the den area. Any influence of the number of individuals within a pack on the home-range size is likely to be obscured by this limitation.

Kill and scat analysis

Data on prey killed by dholes were collected. The pack responsible for the kill was ascertained from the area where the kill was found, with kills found in areas of range overlap between the 2 packs being disregarded. The age of the animal killed was estimated from the dentition of the lower mandibles (Schaller, 1967). Young fawns were often killed and completely consumed, leaving only traces of the animal. In all such instances (fawns actually observed being killed or inferred from trace evidence of fresh kills), the age of the prey was taken to be less than 1 year. Thus our data on kills still underestimate the proportion of fawns in relation to older age classes, as there is a higher chance of fawn kills going undetected.

Dhole scats were collected for identification of prey species. A key prepared by Koppikar & Sabnis (1976, 1977) was used, in addition to our own reference key, to identify the hairs in the scats. Two methods were used to quantify the prey remains in the scat. The first method calculated the index p_i as follows:

$$p_i = \frac{x_i}{\sum_{i=1,n} x_i}$$

where, x_i is the number of scats containing remains of species i and n is the total number of species whose remains were present in all the scats. The occurrences of remains of more than one prey species in a single scat were thus scored as separate occurrences for each of the prey species present. All scat percentages reported are $p_i \times 100$.

The above method is biased in favour of prey species of smaller size because their higher surface to volume ratio relative to larger prey ensures that more hair is passed on in scats for a given weight of prey consumed. We thus followed Floyd, Mech & Jordan (1978) who provide a method for correcting for this bias by carrying out feeding trials in the wolf (*Canis lupus*). We assume that the regression equation used ($y = 0{\cdot}38 + 0{\cdot}02x$, where x is the average weight of an individual of a given prey type and y is the weight in kg of the prey animal per collectable scat) for the wolf is also applicable to the dhole (being a wolf-like canid), with both possibly having similar digestive efficiencies.

Prey distribution and densities

The location of chital (*Axis axis*) herds were monitored on an *ad libitum* basis as frequently as possible. For plotting their distributions on a map, only locations noted before 08:30 h and after 18:30 h were used, as chital tend to aggregate when night approaches and disperse to a certain extent during the day. While useful for getting a picture of distribution, this does not by itself provide statistically robust estimates of animal density.

Line transects, following the method of Burnham, Anderson & Laake (1980), and as applied by Karanth & Sunquist (1992) in a similar forest habitat, are walked extensively in the Mudumalai Sanctuary as part of a programme of censusing large mammal populations. Six transects of 2–4 km each, covering the various habitat types, are each walked twice a month throughout the year. Chital and sambar (*Cervus unicolor*) densities were obtained from Fourier series analysis of line transect data for the year 1991 (Varman & Sukumar, 1993 and unpubl. results). Animals seen on transects were classified according to age and sex. Cattle densities were calculated from records maintained by the Forest Department on permits issued for grazing and our surveys of villages to census cattle numbers.

Statistical analyses of prey selection

Chi-squared tests of independence (Sokal & Rohlf, 1981) were used for different contingency tables set up to test 3 null hypotheses. These null hypotheses were:

1) Numbers and biomass of the 3 major prey species (chital, sambar, and cattle) were killed and consumed in accordance with their availability in a pack's home range. This implies that dholes kill according to availability and do not specifically select any given prey species.
2) Animals less than 1 year old are killed in proportion to their availability in the population.
3) The sex ratio of animals killed by dholes was in accordance with the population sex ratio.

Expected values were based on numbers (or biomass) of prey species, age structures of prey, and sex ratios of prey in the population as determined from line transect data, while observed values were based on occurrences of prey remains in dhole scats, age structures of prey killed, and sex ratios of prey killed, respectively. As non-independence of data tends to produce false rejection of the null hypothesis by the chi-squared test (Kramer & Schmidhammer, 1992), we have considered chi-squared values significant only at the higher probability level of $P < 0{\cdot}01$.

We also carried out Pearson's product moment correlational analyses between pack size and body weight of prey killed using our data and Johnsingh's (1983) data from Bandipur National Park, and between pack size and quantity of food eaten/adult dhole/kill.

Analysis of resource patch utilization

We have watched the Kargudi dhole pack specifically visit areas where chital herds habitually graze and, if the herd is not present or if a hunt is unsuccessful, move on to the next herd. We divided the Kargudi pack's home range into what we call 'resource patches'. A 'resource patch' consists of fixed resting sites where the dhole pack rests between hunts and at nights and the herds which it hunts (Fig. 1). The resting sites are either located in grassy meadows or on small rocky hillocks. The pack travels from these resting sites to fixed chital

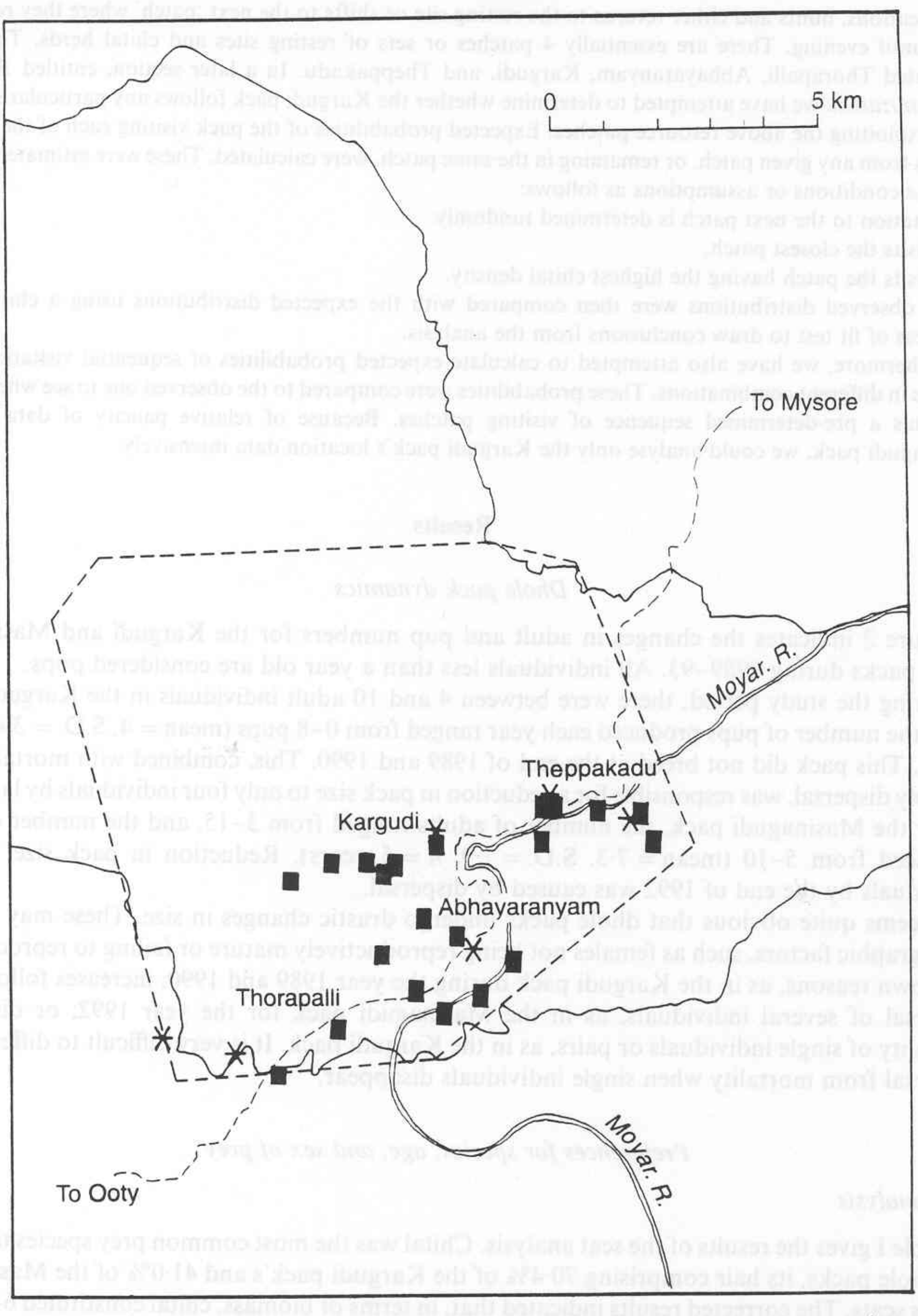

FIG. 1. Map showing the four major 'resource patches' of the Kargudi dhole pack. Each resource patch consists of chital herds (■) and resting sites of the dhole pack (★). The home range of the pack (-----), as determined by the minimum convex polygon method, is also shown. Visits by the pack to the northern part of the home range are relatively rare.

herd locations, hunts and either returns to the resting site or shifts to the next 'patch' where they rest once again until evening. There are essentially 4 patches or sets of resting sites and chital herds. These are designated Thorapalli, Abhayaranyam, Kargudi, and Theppakadu. In a later section, entitled *Resource patch utilization*, we have attempted to determine whether the Kargudi pack follows any particular strategy when exploiting the above resource patches. Expected probabilities of the pack visiting each of the 3 other patches from any given patch, or remaining in the same patch, were calculated. These were estimated from 3 separate conditions or assumptions as follows:

a) Visitation to the next patch is determined randomly.
b) It visits the closest patch.
c) It visits the patch having the highest chital density.

The observed distributions were then compared with the expected distributions using a chi-squared goodness of fit test to draw conclusions from the analysis.

Furthermore, we have also attempted to calculate expected probabilities of sequential visitations to 3 patches in different combinations. These probabilities were compared to the observed one to see whether the pack has a pre-determined sequence of visiting patches. Because of relative paucity of data for the Masinagudi pack, we could analyse only the Kargudi pack's location data intensively.

Results

Dhole pack dynamics

Figure 2 indicates the changes in adult and pup numbers for the Kargudi and Masinagudi dhole packs during 1989–93. All individuals less than a year old are considered pups.

During the study period, there were between 4 and 10 adult individuals in the Kargudi pack, while the number of pups produced each year ranged from 0–8 pups (mean = 4, S.D. = 3·4, $n = 5$ years). This pack did not breed at the end of 1989 and 1990. This, combined with mortality and possibly dispersal, was responsible for a reduction in pack size to only four individuals by late 1991.

For the Masinagudi pack, the number of adults ranged from 3–15, and the number of pups produced from 5–10 (mean = 7·3, S.D. = 1·9, $n = 5$ years). Reduction in pack size to four individuals by the end of 1992 was caused by dispersal.

It seems quite obvious that dhole packs undergo drastic changes in size. These may include demographic factors, such as females not being reproductively mature or failing to reproduce for unknown reasons, as in the Kargudi pack during the year 1989 and 1990; increases followed by dispersal of several individuals, as in the Masinagudi pack for the year 1992; or dispersal/mortality of single individuals or pairs, as in the Kargudi pack. It is very difficult to differentiate dispersal from mortality when single individuals disappear.

Preferences for species, age, and sex of prey

Scat analysis

Table I gives the results of the scat analysis. Chital was the most common prey species taken by the dhole packs, its hair comprising 70·4% of the Kargudi pack's and 41·0% of the Masinagudi pack's scats. The corrected results indicated that, in terms of biomass, chital constituted 61·1% of the Kargudi pack's and 33·4% of the Masinagudi pack's prey consumption. Sambar was an equally important prey for the Masinagudi pack, constituting 36·1% of biomass consumed, while it was relatively less important (32·4%) than chital for the Kargudi pack. Similarly, the Masinagudi pack preyed upon cattle to a substantial extent (25·6% of prey biomass), unlike

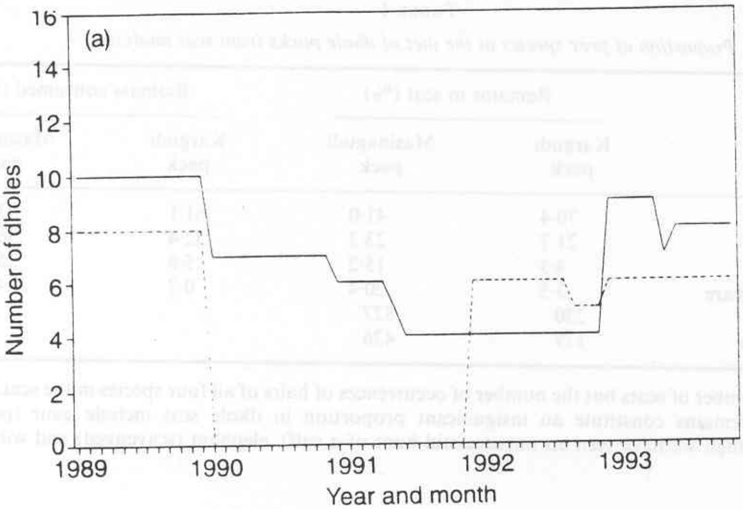

FIG. 2. Changes in the number of adults (——) and pups (.........) during the study period in: (a) the Kargudi dhole pack: and (b) the Masinagudi dhole pack.

the Kargudi pack (5·8%). The black-naped hare (*Lepus nigricollis*) was insignificant for the Kargudi pack (0·7%) but more commonly consumed by the Masinagudi pack (4·9%). It is thus seen that the Masinagudi pack had a more varied diet while the Kargudi pack relied substantially on just one prey species.

Table II gives the density and biomass of the principal prey species within the home ranges of the two dhole packs. Chital densities are higher than those of sambar in both regions, although sambar maintain a higher biomass than chital in the Kargudi pack's range. Cattle density is very high in the Masinagudi pack's range where grazing is permitted.

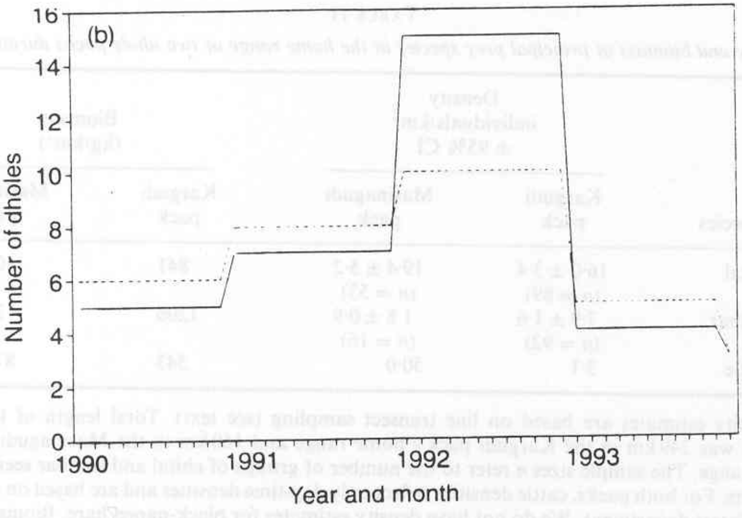

FIG. 2b

TABLE I

Proportion of prey species in the diet of dhole packs from scat analysis

	Remains in scat (%)		Biomass consumed (%)	
Prey species	Kargudi pack	Masinagudi pack	Kargudi pack	Masinagudi pack
1. Chital	70·4	41·0	61·1	33·4
2. Sambar	21·7	23·3	32·4	36·1
3. Cattle	4·3	15·2	5·8	25·6
4. Black-naped hare	3·5	20·4	0·7	4·9
Sample size (*n*)	230	827		
Number of scats	179	426		

n is not the number of scats but the number of occurrences of hairs of all four species in the scat. Other species whose remains constitute an insignificant proportion in dhole scat include gaur (possibly scavenged, although we have seen an unsuccessful hunt of a calf), elephant (scavenged) and wild boar (hunted)

A chi-squared test of independence showed that neither pack killed prey in proportion to prey availability ($\chi^2 = 19{\cdot}9$ for the Kargudi pack and 2257 for the Masinagudi pack, $d.f. = 2$, $P < 0{\cdot}005$). The Kargudi pack killed more chital ($\chi^2 = 7{\cdot}1$, $d.f. = 1$, $P < 0{\cdot}01$), and less cattle ($\chi^2 = 9{\cdot}4$, $d.f. = 1$, $P < 0{\cdot}005$) than expected, while the number of sambar killed did not differ significantly from its proportion in the population ($\chi^2 = 3{\cdot}4$, $d.f. = 1$, $P > 0{\cdot}05$). The Masinagudi pack killed more chital ($\chi^2 = 142{\cdot}3$, $d.f. = 1$, $P < 0{\cdot}005$) and sambar ($\chi^2 = 1870$, $d.f. = 1$, $P < 0{\cdot}005$), but less cattle ($\chi^2 = 244{\cdot}4$, $d.f. = 1$, $P < 0{\cdot}005$) than expected.

Once again, neither pack consumed prey in proportion to biomass availability of the prey species ($\chi^2 = 118{\cdot}2$ for the Kargudi pack and 3475 for the Masinagudi pack, $d.f. = 2$, $P < 0{\cdot}005$). The Kargudi pack consumed a greater biomass of chital ($\chi^2 = 74{\cdot}8$,

TABLE II

Density and biomass of principal prey species in the home range of two dhole packs during 1991

	Density individuals/km^2 ± 95% CI		Biomass (kg/km^2)	
Prey species	Kargudi pack	Masinagudi pack	Kargudi pack	Masinagudi pack
1. Chital	16·0 ± 3·4 ($n = 89$)	19·4 ± 5·2 ($n = 53$)	841	1082
2. Sambar	7·9 ± 1·6 ($n = 92$)	1·8 ± 0·9 ($n = 16$)	1206	281
3. Cattle	3·1	50·0	543	8750

Density estimates are based on line transect sampling (see text). Total length of transect walked was 249 km in the Kargudi pack's home range and 160 km in the Masinagudi pack's home range. The sample sizes *n* refer to the number of groups of chital and sambar seen in the transects. For both packs, cattle densities reflect only day-time densities and are based on records of the forest department. We do not have density estimates for black-naped hare. Biomass/km^2 was calculated using the weights and proportions of animals in the different age classes sambar kills. Because of this low sample size, we pooled data from both packs to test for preference for the sexes. The population level ratios of male to female were 1:2·6 for chital and 1:3·1 for sambar. Male chital seem to be killed in greater proportion than their availability in the population; this is, however, not statistically significant at a higher significance level ($\chi^2 = 6\cdot1$, $d.f. = 1$, $0\cdot05 > P > 0\cdot01$). Female chital ($\chi^2 = 2\cdot6$, $d.f. = 1$, $P > 0\cdot05$), as well as male ($\chi^2 = 0\cdot72$, $d.f. = 1$, $P > 0\cdot05$) and female sambar ($\chi^2 = 0\cdot23$, $d.f. = 1$, $P > 0\cdot05$) killed, did not vary significantly from their proportions in the population.

For correlating biomass of prey killed by the size of the pack responsible for the kill, we used mean weights of the age classes of animals of three prey species (given in Table IV). Data from 136 dhole kills collected in this study, along with 93 kills collected by Johnsingh (1983) in nearby Bandipur National Park were used. There was no correlation between pack size and body weight of prey killed (for Kargudi pack: Pearson's product moment correlation coefficient $r = 0\cdot167$, $d.f. = 54$, $P > 0\cdot05$; for Masinagudi pack: $r = 0\cdot030$, $d.f. = 78$, $P > 0\cdot05$; for Bandipur pack: $r = 0\cdot031$, $d.f. = 91$, $P > 0\cdot05$; for combined data: $r = 0\cdot066$, $d.f. = 228$, $P > 0\cdot05$). When we examined Johnsingh's (1980) data on pack size and quantity of food (in kg) eaten/adult dhole/kill, we found a negative correlation between these two variables (Pearson's $r = -0\cdot267$, $d.f. = 87$, $P < 0\cdot01$). These results indicate that larger packs often result in smaller per capita yield of meat for a given time period as compared to a smaller pack.

Owing to difficulties in observing hunts from start to finish under conditions of poor visibility in forest, we have limited data on how pack size may influence success rate. Out of 11 hunts (the prey being two sambar adult females and three fawns, one chital adult male, one adult female and four fawns) observed completely, in only two cases were pack members positioned in a manner which could be interpreted as restricting prey movement or escape options. In the other nine hunts only 1–3 hunters were seen, even though the pack had 4–11 adults. We, therefore, believe that the number of hunters in a pack may be limited and that success rate may not necessarily increase with pack size.

Home-range analysis

The Kargudi pack's home range (83·3 km^2) during the study period (April 1990–December

TABLE IV

Weight of different age classes of prey species. Modified from Johnsingh (1983)

Prey species	Weight (kg)
1. Chital fawn	
Small (<6 months)	15
Big (>6 months)	20
2. Chital female (>1 year)	50
3. Chital male (>1 year)	75
4. Sambar fawn (< 1 year)	50
5. Sambar female (> year)	150
6. Sambar male (>1 year)	225
7. Cattle calf (<1 year)	45
8. Cattle adult (>1 year)	175
9. Black-naped hare (Our estimate)	3

$d.f. = 1$, $P < 0{\cdot}005$) but less sambar ($\chi^2 = 11{\cdot}9$, $d.f. = 1$, $P < 0{\cdot}005$) and cattle ($\chi^2 = 31{\cdot}5$, $d.f. = 1$, $P < 0{\cdot}005$) than what was available. The Masinagudi pack, however, seemed to consume a greater biomass of sambar ($\chi^2 = 2853$, $d.f. = 1$, $P < 0{\cdot}005$) and chital ($\chi^2 = 358{\cdot}4$, $d.f. = 1$, $P < 0{\cdot}005$) but less cattle ($\chi^2 = 263{\cdot}5$, $d.f. = 1$, $P < 0{\cdot}005$) than what was available.

We also carried out the analysis by omitting cattle as these may not be 'typical' prey under natural conditions and predation success may also depend on factors such as presence of graziers, time of entry of cattle into the forest, and so on. It was found that neither pack killed according to prey availability ($\chi^2 = 81{\cdot}4$ for the Kargudi pack and $221{\cdot}2$ for the Masinagudi pack, $d.f. = 1$, $P < 0{\cdot}005$). The Kargudi pack killed more chital ($\chi^2 = 50{\cdot}0$, $d.f. = 1$, $P < 0{\cdot}005$) but less sambar ($\chi^2 = 31{\cdot}4$, $d.f. = 1$, $P < 0{\cdot}005$) than expected. In contrast, the Masinagudi pack killed less chital ($\chi^2 = 50{\cdot}9$, $d.f. = 1$, $P < 0{\cdot}005$) but more sambar than expected ($\chi^2 = 170{\cdot}3$, $d.f. = 1$, $P < 0{\cdot}005$). A similar result is obtained when we consider biomass of the two prey species.

Analysis of kills

Table III shows the age distributions of chital and sambar in the population and those of prey killed by the two dhole packs. Over 80% of the chital killed by the Kargudi pack was less than a year old, while chital fawns constituted only 61% of animals taken by the Masinagudi pack. Both packs predominantly took sambar less than a year old (76 and 67% for the Kargudi and Masinagudi packs, respectively).

We do expect a bias in this kind of analysis. Chital and sambar fawns are eaten almost entirely; often only the lower jaws remain, making detection of such kills unlikely. Our results are thus entirely opposite to what can be expected from such a sampling bias, corroborating the fact that the two packs do prey predominantly on younger animals of both species. A chi-squared test of independence showed that, for both dhole packs, the proportion of chital and sambar fawns (< one year old) killed was much greater than their availability in the population (see Table III for chi-squared values).

It was possible to sex only 33 (17 male and 16 female) chital kills and 25 (4 male and 21 female)

TABLE III

Age distribution of prey species in the population and of kills by two dhole packs

Prey species and age class	No. individuals in population (%)	No. individuals in kills (%)	χ^2 value	P ($d.f. = 1$)
(a) Kargudi pack				
Chital (< 1 yr)	14·1	81	169·2	< 0·005
Chital (> 1 yr)	85·9	19	27·7	< 0·005
Sample size (n)	*1776*	*75*		
Sambar (< 1 yr)	13·5	76	99·7	< 0·005
Sambar (> 1 yr)	86·5	24	15·6	< 0·005
Sample size (n)	*503*	*34*		
(b) Masinagudi pack				
Chital (< 1 yr)	11·9	61	36·5	< 0·005
Chital (> 1 yr)	85·1	39	4·9	< 0·05
Sample size (n)	*193*	*18*		
Sambar (< 1 yr)	15·8	67	14·8	< 0·005
Sambar (> 1 yr)	84·2	33	2·8	> 0·05
Sample size (n)	*38*	*9*		

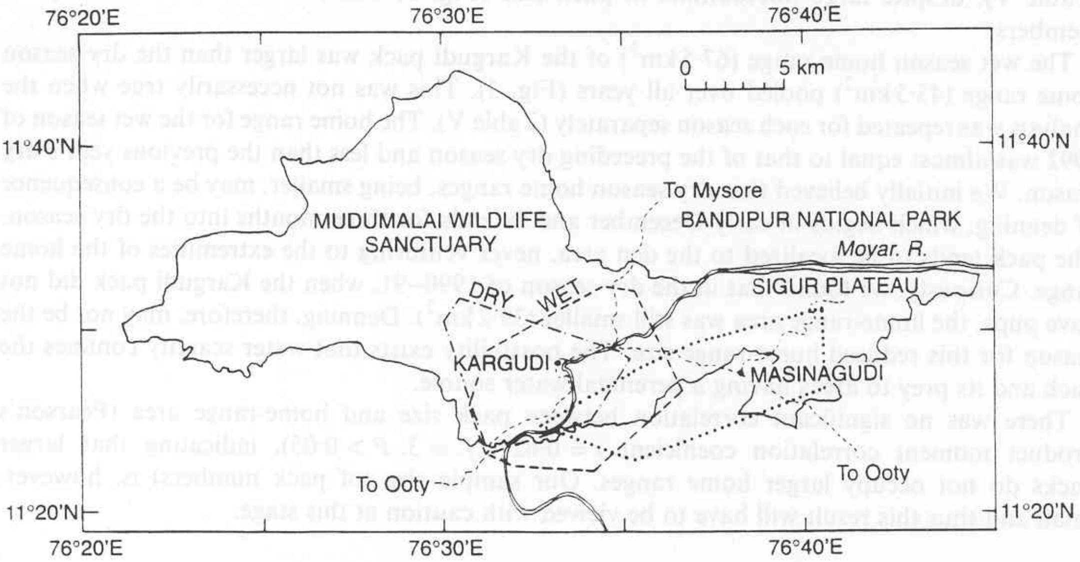

FIG. 3. Map of the study area showing the home ranges of the Kargudi and Masinagudi dhole packs. Home ranges are shown separately for dry (-------) and wet (-------) seasons for the Kargudi pack. For the Masinagudi pack (··········) the total home range for the study period is shown.

1992) was larger than that of the Masinagudi pack's home range (54·2 km^2) (Table V, Fig. 3). Our results should be taken as minimum home-range sizes as these are based on resightings of identified packs and not on monitoring through radio-telemetry.

Home-range areas for the Kargudi pack tended to be constant for each of the years 1990–92

TABLE V

Home-range areas of dhole packs

	Home range (km^2)	Number of days of location
KARGUDI PACK		
Total (1990–1992)	83·3	276
1990	52·9	79
1991	61·7	139
1992	53·9	57
Wet season 1990	52·6	69
Dry season 1991	39·2	26
Wet season 1991	48·4	119
Dry season 1992	27·4	9
Wet season 1992	27·9	50
Pack size 7	52·9	79
Pack size 6	34·4	20
Pack size 5	20·7	50
Pack size 4	43·1	69
Pack size 10	53·9	53
MASINAGUDI PACK		
Total (1990–92)	54·2	103

(Table V), despite large fluctuations in pack size (Fig. 3) and a certain turnover of pack members.

The wet season home range ($67{\cdot}5\,\mathrm{km}^2$) of the Kargudi pack was larger than the dry season home range ($43{\cdot}5\,\mathrm{km}^2$) pooled over all years (Fig. 3). This was not necessarily true when the analysis was repeated for each season separately (Table V). The home range for the wet season of 1992 was almost equal to that of the preceding dry season and less than the previous year's dry season. We initially believed that dry season home ranges, being smaller, may be a consequence of denning, which begins in early December and extends for three months into the dry season. The pack tends to be localized to the den area, never venturing to the extremities of the home range. Curiously, we found that in the dry season of 1990–91, when the Kargudi pack did not have pups, the home-range area was still smaller ($39{\cdot}2\,\mathrm{km}^2$). Denning, therefore, may not be the reason for this reduced home-range size. The possibility exists that water scarcity confines the pack and its prey to areas having a perennial water source.

There was no significant correlation between pack size and home-range area (Pearson's product moment correlation coefficient $r = 0{\cdot}62$, $d.f. = 3$, $P > 0{\cdot}05$), indicating that larger packs do not occupy larger home ranges. Our sample size (of pack numbers) is, however, small and thus this result will have to be viewed with caution at this stage.

Resource patch utilization

Strings of dhole locations from consecutive sightings were obtained for the Kargudi pack. These strings were considered discontinuous when two consecutive locations were recorded after a gap of more than two days. In such cases, the exact sequence of visiting resource patches could not be confirmed as there may have been a third, unrecorded location in-between. From the location data, it was possible to reconstruct the sequence by which the pack visited the four patches within its home range (Fig. 1).

If the pack is in patch i (where $i = 1, 4$; the four possible patches the pack can visit) on day t, on day $t + 1$ it can either visit another patch j ($j = 1, 4$, $j \neq i$) or remain in the same patch ($j = i$). Four null hypotheses were tested with this basic scenario.

HYPOTHESIS (1): The number of visits made to each of the four different patches was equal.

The probabilities of visitations to each of the four different patches were calculated by dividing the number of visits made to each patch by the total number of visits made to all patches to give us p_i, $i = 1, 4$. These will hence be termed as the 'preference probabilities'. These were used to obtain the observed values. The expected values were calculated assuming that the total number of visits were apportioned equally among the four patches. These were compared in a chi-squared goodness of fit test and it was found that the observed distribution did not fit the expected distribution ($\chi^2 = 116{\cdot}5$, $d.f. = 2$, $P < 0{\cdot}001$), indicating that the pack has a preference for certain patches (Kargudi = 104 >Theppakadu = 60 >Abhayaranyam = 38 >Thorapalli = 37, where the numbers are the visits to each patch). On examining the deviations of the observed from the expected in a cell by cell manner, we find that the observed number of times the pack visits Thorapalli ($\chi^2 = 8{\cdot}66$, $d.f. = 1$, $P < 0{\cdot}0125$, Bonferroni's adjustment), Abhayaranyam ($\chi^2 = 7{\cdot}9$, $d.f. = 1$, $P < 0{\cdot}0125$, Bonferroni's adjustment) and Kargudi ($\chi^2 = 32{\cdot}8$, $d.f. = 1$, $P < 0{\cdot}0125$, Bonferroni's adjustment) deviate significantly from the expected.

HYPOTHESIS (2): If the pack is in patch i the probability of moving into each of four patches j ($j = 1, 4$; one outcome is to remain in the same patch) is the 'preference probability' p_j of j.

Each patch i was fixed and the number of times the pack either stayed in the patch on day $t + 1$

or moved to each of the other patches j ($j = 1, 4$) was determined (Table VIb). The total number of times the pack left patch i was multiplied by each of the 'preference probabilities' p_j to give the expected number of visits to each of the patches j. The observed distribution did not fit the expected distribution, indicating that, after being in patch i, the pack does not necessarily go to the patch it prefers the most ($\chi^2 = 59{\cdot}5$, $d.f. = 9$, $P < 0{\cdot}001$).

HYPOTHESIS (3): The pack has the highest probability of moving from patch i to the nearest patch j.

The distance between two continuous patches i and j was assumed to be the linear distance between the main resting sites in either patch. This was considered more realistic as the pack usually tends to move from one resting site to another. The distance between two non-contiguous patches i and k was the sum of the distances between the continuous patches i and j and between j and k (measured between resting sites). It was assumed that the probabilities of visiting each of the patches j after being in patch i is inversely proportional to the distance between the two patches.

Various powers of $1/d_{ij}$ were tested for correlation with the number of times the pack went from each patch i to j, n_{ij} ($i, j = 1, 4$, $i \neq j$). It was found that $1/d^{0\cdot1}$ (and powers of $d < 0{\cdot}1$) correlated well with n_{ij} (Pearson's $r = 0{\cdot}60$, $d.f. = 10$, $P < 0{\cdot}05$). The following expression was used to calculate the probabilities of going from patch i to j:

$$\begin{gathered} i \neq j \\ \Sigma p_{ij} = 1 \\ i = 1, 4 \\ \text{where } p_{ij} = (1/d_{ij})^{0\cdot1}\, s \end{gathered} \qquad (1)$$

where, s is the reciprocal of the sum of $1/d_{ij}{}^{0\cdot1}$, $i \neq j$, for each i. The total number of times the pack left patch i was then multiplied by each of the above probabilities to give us the expected number of times the pack visited each of the patches j after being in patch i (Table VIc). The observed values were the same as in the previous case (Table VIa). The observed distribution did not fit the expected one ($\chi^2 = 17{\cdot}4$, $d.f. = 6$, $P < 0{\cdot}001$). It can be concluded that the probabilities of the pack moving from patch i to patches j is not based on how far each patch j is from patch i.

HYPOTHESIS (4): We finally tested whether, if the pack is in patch i, having a relative chital density D_i, it is most likely to move to the patch j having the highest relative chital density D_j among the patches.

The relative chital densities of the four patches in ascending order (Thorapalli < Theppakadu < Kargudi < Abhayaranyam) are 1 : 2·47 : 2·58 : 3·14. The expected probabilities of visiting each of the patches j were calculated as above, by substituting $1/d_{ij}$ with:

$$D_j/D_i \qquad (2)$$

Once again powers of equation 2 were correlated with the numbers of times the pack went from each patch i to j, $i \neq j$. Here it was found that the powers of the above expression were not particularly more correlated with n_{ij} than the unmodified expression (Pearson's $r = 0{\cdot}14$, $P > 0{\cdot}05$, $d.f. = 10$). The expression was left unmodified in the next analysis. Each of the probabilities obtained hence were multiplied by the total number of times the pack left patch i to give us the expected number of times the pack visited patches j if they were more likely to visit the densest patch (Table VId). The observed values were the same as above. The observed

TABLE VI

Expected and observed values for the four null hypotheses tested on resource patch utilization. THR = Thorapalli, ABA = Abhayaranyam, KAR = Kargudi, THA = Theppakadu

(a) Observed number of times the pack leaves patch i and goes to the patches j

	j			
	THR	ABA	KAR	THA
THR	14	7	5	2
ABA	2	9	13	4
KAR	8	6	49	20
THA	3	9	17	22

(b) Expected number of times when pack is most likely to go to patch j with 'preference probability' p_j

	THR	ABA	KAR	THA
THR	4·34	4·45	12·18	7·03
ABA	4·34	4·45	12·18	7·03
KAR	12·85	12·20	36·12	20·84
THA	7·90	8·11	22·19	12·80

(c) Expected number of times when pack is most likely to go to nearest patch j from patch i

	THR	ABA	KAR	THA
THR	na	6·38	4·56	3·04
ABA	4·39	na	10·45	4·18
KAR	5·61	18·70	na	12·34
THA	10·02	4·55	15·02	na

(d) Expected number of times when pack is most likely to go to next patch having the highest chital density

	THR	ABA	KAR	THA
THR	na	3·68	8·61	2·69
ABA	1·12	na	13·78	4.30
KAR	3·32	17·84	na	12·86
THA	1·58	8·34	19·55	na

(e) Chi-squared analysis on triplet sequences

Class	Observed	Expected	Chi-squared value
(1) Forward sequences	31	21·37	4·33
(2) Backward sequences	29	24·37	0·89
(3) Same patch	42	15·03	48·39
(4) Others	45	86·22	19·07
Total	147	147	73·31

TABLE VI (*cont.*)

(f) Residence time (days) of the pack in the four patches

	Mean ± S.D.	Median (range)	Sample size *n*
THR	2·44 (±0·83)	2·0 (1–3)	10
ABH	1·90 (±1·30)	2·5 (1–4)	9
KAR	3·00 (±1·88)	3·0 (1–7)	30
THA	2·13 (±1·13)	2·5 (1–6)	15

As residence times in patches may not be normally distributed we used the non-parametric Mann–Whitney U-test to compare time spent in a given patch with the time spent in each of the other patches separately. All the six comparisons were statistically not significantly different ($P > 0{\cdot}05$)

distribution did not fit the expected distribution, indicating that the pack was not more likely to visit the densest prey patch from patch i ($\chi^2 = 23{\cdot}8$, $d.f. = 6$, $P < 0{\cdot}001$).

We thus concluded that the pack, after leaving patch i, was not more likely to visit the most preferred patch, the closest patch or a patch with higher chital densities. What are the other parameters possibly assessed when they go to the next patch? The data were scanned for all possible triplets, e.g. Kargudi, Theppakadu, and Thorapalli would constitute a sequence of visitations over a 3-day period. If the pack is in a given patch i on day t it has four possible patches to go to on day t+1. Alternatively, it could remain in the same patch on day t+1. On day t+2 it has four more possibilities: either remain in the same patch where it was on day t+2; return to the patch where it was on day t; or move on to the two remaining patches. Thus we get 4^3 different combinations and for each combination we calculated what can be called transitional probabilities. To determine the observed values for these 64 different triplets we tallied the number of times the pack followed each of the triplet sequences. The expected values were calculated in the following manner. If the pack left patch i on day t n_i times, the expected number of times it went to patch j and patch k were $n_i p_j p_k$, where p_j and p_k are the 'preference probabilities' of visiting patches j and k.

The triplet sequences were grouped into four classes (Table VIe). The first class had all triplet sequences where visitations followed the order Thorapalli, Abhayaranyam, Kargudi, and Theppakadu. These four patches are arranged in a linear sequence with Thorapalli occupying one extremity of the home range followed by Abhayaranyam, Kargudi, and finally Theppakadu occupying the other end of the pack's home range. The second class had triplet sequences following the above order in reverse. The third class had instances where the pack remained in the same patch over three consecutive sightings. All other triplet sequences were grouped into the fourth class. This gave us a 4 × 2 contingency table. On performing a chi–squared goodness of fit test, we found the chi–squared value to be significant ($\chi^2 = 73{\cdot}3$, $d.f. = 3$, $P < 0{\cdot}05$). To check what accounted for this significant value, we examined each cell separately. The third class accounted for the highest chi–squared value ($\chi^2 = 48{\cdot}4$, $d.f. = 1$, $P < 0{\cdot}025$, Bonferroni's adjustment). The fourth class accounted for the second highest value, but here the observed value was far less than the expected one. The interesting finding was that the first class had a significant chi–squared value ($\chi^2 = 4{\cdot}33$, $d.f. = 1$, $0{\cdot}05 < P < 0{\cdot}025$, Bonferroni's adjustment).

The deviation between the observed and the expected was positive. The second class, however, had a non-significant value ($\chi^2 = 0{\cdot}89$, $d.f. = 1$, $P > 0{\cdot}05$, Bonferroni's adjustment). It appears that the pack has a tendency to follow the above sequence in the forward direction but not in the reverse.

It was also observed that there was no statistically significant difference in the average residence time of the pack in the four patches (see Table VIf for details).

Discussion

The highly social canids such as African hunting dogs, wolves, and dholes are rather unique among carnivores in that social groups, rather than being relatively loose aggregations of individuals, have a rigid social structure where individuals interact through fixed dominance hierarchies. Their other striking attribute is the high level of co-operative behaviour, such as co-operative breeding and hunting (Moehlman, 1986).

Several reasons have been advanced to explain the evolution of co-operative hunting. Packer & Ruttan (1988) give a theoretical framework for the evolution of co-operation among two interacting animals. Co-operation can be an ESS (Evolutionary Stable Strategy) only when the increased performance of a co-operative pair is greater than the disadvantage of dividing the prey in half. Otherwise, individuals would be better off hunting alone. The improved performance could come from increased prey encounter rates, increased hunting success by pairs or decreased hunting costs. Fanshawe & Fitzgibbon (1993) observed enhanced group sizes in African hunting dogs hunting wildebeest as a consequence of individual hunting success being low. On the other hand, Thompson's gazelle were hunted solitarily or by pairs of dogs. Increased efficiency while hunting larger prey may thus foster the evolution of enhanced canid groups.

We, however, wish to consider a more basic explanation for the rudiments of group formation which may have greater relevance to our results. An important aspect of our study is that we have incorporated information on distribution and density of prey species. Chital tend to live in large, loose herds which are patchily distributed. In contrast, sambar live in much smaller aggregations of individuals, which are more uniformly distributed in their habitat. We, unfortunately, do not have information on how dhole packs utilize sambar as a resource, which is a point of considerable interest, but on considering chital distributions it is appropriate at this stage to explore the predictions of the Resource Dispersion Hypothesis (RDH) as it relates to canid social evolution (Macdonald, 1983). A basic tenet of this hypothesis is that resources should be dispersed in patches which vary both spatially and temporally in richness. This seems to be the case with chital resources. Temporal variation occurs across seasons as mean group sizes of chital increase during the wet season and reduce during the dry season (K. S. Varman & R. Sukumar, unpubl. results). The large variation in chital densities across the home range constitutes the spatial variation in resources (Macdonald, 1983).

On considering the patch-linked exploitation of resources, dissecting out the underlying factors governing movement of the Kargudi pack appears to be rather difficult, although certain broad conclusions can be made from the analysis of patch utilization. It could be possible that the longer the pack remains in the same patch, the more vigilant chital may get, making future hunting difficult. Thus the pack is often forced to change patches when hunting success drops. Hunting success is variable across patches and within patches temporally. This may account for the result that the mean time spent in the four different patches do not vary significantly and that the plausible factors we tested, influencing which patch to go to next, were not applicable. The tendency to visit patches in a particular sequence (Thorapalli, Abhayaranyam, Kargudi, and Theppakadu) merits further attention. There is no increasing prey gradient in the above direction. Visiting in the forward sequence avoids revisiting and gives the pack potentially fresh patches to exploit. On the return, however, the tendency may be to return to the first patch through a sequence of patches which may not be predetermined. In short, the pack moves in a circle, predictably in the forward direction and less predictably on the return. It is also quite plausible that, on account of increased vigilance through continued hunting and consequent drop in hunting success, alternative resource patches within a pack's home range are required to ensure steady long-term yields.

One prediction of the RDH is that home-range areas should not increase as a function of group size. The advantage of numbers is lost if this were to happen because resource patches within the basic pair's natal home range could be guarded more efficiently if more individuals were to be taken on. We found that home-range areas do not increase with pack size. Even though our sample size is small, we do have the corroborating result that home-range areas remained constant through all study years, despite large fluctuations in pack size and a certain turnover of pack individuals.

Another important prediction of the RDH is that, for carnivore groups, the existence of large group sizes may not necessarily be fostered by the advantages of a large number of group members hunting co-operatively. This certainly seems to be true when we consider that dholes prefer to hunt fawns (of both chital and sambar). A similar preference for chital fawns by dholes was observed by Johnsingh (1983) at Bandipur National Park. We observed some hunts where as few as two dholes brought down fawns which were shared by a majority of pack members. In fact, we have even observed a single dhole killing a mouse deer (*Tragulus memmina*) and consuming it entirely alone. A significant proportion of black-naped hare in the Masinagudi pack's diet, a prey animal which could be taken by a single dhole, testifies to the idea that, in terms of providing minimum nutritional requirements, pack sizes greater than two may not be essential. This could be compared to African hunting dogs hunting gazelles solitarily or in pairs. One, however, does not belittle instances of co-operative effort being used to hunt sambar adults or when dholes use the flushing strategy (Johnsingh, 1983) to hunt small prey such as chital fawns.

The lack of correlation between biomass of prey killed and pack size, however, makes us believe that larger packs often result in smaller per capita yield of meat as compared to smaller packs. This may make living in larger packs more disadvantageous. Increased food intake as a consequence of enhanced group size may therefore not be a facilitating force for the evolution of group living in dholes. The issue of whether this disadvantage is offset by the conditions for co-operation to be an ESS is of considerable theoretical interest.

If our results are typical for most dhole packs, the manner in which packs assess temporal changes in hunting success, for decisions on whether to leave a patch or which patch to go to next, may have evolved to ensure steady long-term gains. For this strategy to be effective, a pack needs a large home range, with resource patches (chital herds in our case) within, which are expected to vary temporally in yield. Therefore, if a pack incorporates more patches within its home range, it could ensure steady long-term yields. A problem is that the habitat may not offer an endless continuum of such patches. A given habitat will have a carrying capacity for the number of packs it can support. The mortality of young among litters (sizes of litters can be large, Table I) is thought to be low (ABV, unpubl. results). This sometimes may result in large-sized packs (for instance, the Masinagudi pack in the years 1991 and 1992; a pack of 26 dholes recorded in the

Satyamangalam Forest Division in 1981 by RS). Easy dispersal may not be possible because of the lack of a continuum of patches caused by natural and artificial habitat boundaries (such as for the Masinagudi pack), poor habitat for prey, etc. Sub-adults, which are generally the ones to disperse, may thus be forced to stay on in their natal pack owing to the lack of areas to disperse to, and possibly owing to the presence of other packs in adjoining habitats.

We thus speculate that dholes form packs not for the purposes of increased efficiency during hunting, but because of dispersion of resources and constraints on dispersal by the paucity of ideal habitats. Staying on in the natal home range may therefore be the best strategy. In such a case, other social advantages, such as benefits from defence of kills, co-operative care of young, and allogrooming may then act as further cohesive forces to maintain large dhole groups.

This study was funded by the Ministry of Environment and Forests, Government of India. We thank the Forest Department of Tamil Nadu for permission to carry out research in Mudumalai Sanctuary. K. Surendra Varman provided the data on prey densities and population structure. We also thank K. Ullas Karanth, A. J. T. Johnsingh, N. V. Joshi, K. N. Ganeshaiah and Anindya Sinha for useful discussions and M. Siddhan and R. Shivannan for field assistance. An anonymous referee provided valuable comments on an earlier version of this manuscript.

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