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On diet, foraging behaviour and interspecific food competition of jackals in the Serengeti National Park, East Africa

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Abstract

Studied the diet, foraging behaviour and interspecific food competition in black-backed and golden jackals (*Canis mesomelas* Schreber and *C. aureus* L.) in the Serengeti National Park, Tanzania. Both species gathered invertebrates and fruits and hunted birds and small mammals up to the size of gazelle fawns. Combined data of both species showed that pairs were more than twice as successful as single individuals in gazelle fawn hunts. The jackals frequently lost prey to scavengers. Behavioural adaptations against losing prey are described and possible reasons for the rarity of pack hunting are discussed.

1 Introduction

Jackals are possible the most common of the larger carnivores in Africa and some parts of Asia, yet they have not attracted the attention of biologists as much as the group hunters, i.e. lions, spotted hyaenas, African wild dogs and wolves. However, jackals live in pairs and family groups and are often seen hunting and foraging in pairs (van der Merwe 1953; Wyman 1967; van Lawick 1970; Hendrichs 1972). Since pair hunting offers opportunities for co-operation, it seemed worthwhile

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following up the study by WYMAN (1967) to see whether pair hunts are more successful than hunts of single jackals. This might shed some light on the ecological significance of the jackals' social organization.

Previous studies of jackal food habits have been conducted mainly in South Africa (VAN DER MERWE 1953; GRAFTON 1965; BOTHMA 1966, 1971; ROWE-ROWE 1976), so a further objective was to compare food habits of jackals in the Serengeti with this work. Jackals scavenge from kills of larger carnivores when the opportunity arises, but they also often lose self-caught prey to other scavengers. Competition over dead prey is considerable in the Serengeti and in other areas, where meat-eaters are numerous. It was argued elsewhere (LAMPRECHT 1978) that this type of food competition influences the jackals feeding ecology, hunting behaviour and social organization.

2 Animals, study areas and methods

Black-backed jackals, *Canis mesomelas* Schreber, and golden jackals, *C. aureus* L., live in pairs or family groups. *C. mesomelas* were mostly seen in clearings of the wooded savanna (woodland), along the woodland border, and in open tall grass areas. These were also their breeding habitats. During the wet season, November to April, *C. mesomelas* were occasionally observed on the open short grass plains, the typical breeding habitat of *C. aureus*. During the dry season *C. aureus* were sometimes seen in the tall grass areas around Seronera, which border the woodlands. The main study areas are indicated in Fig. 1. The Serengeti plains are famous for marked seasonal changes in the animal population due to seasonal migration of enormous herds of zebra and wildebeest. Detailed information on features of the Serengeti ecosystem can be obtained from ANDERSON and TALBOT (1965), HENDRICHS (1970), BELL (1971), KRUUK (1972), SCHALLER (1972), and SINCLAIR (1974).

Data were collected between May 1972 and July 1974. D. SCHMIDL kindly contributed more observations until March 1975. Information on hunting, feeding and competition was obtained by direct observation. After having been followed by a Landrover for a few hours, most jackals stopped showing signs of uneasiness when approached as close as 15—30 m. At night they did not seem disturbed by the headlights of the car.

Data on food composition were collected in 3 ways:

1. Direct observation: Food items could be easily identified, when the jackals were hunting gazelles or scavenging on zebra or wildebeest carcasses. Small mammals (e.g. rodents) or arthropods were more difficult, but occasional observations led to an elaboration of the qualitative list of food items (Table 1).
2. Analysis of stomach contents of 6 *C. mesomelas* and 1 *C. aureus*.
3. Faecal analysis: When individuals were observed defaecating, the faeces were collected, if it did not interfere with other types of observations. The droppings were soaked in water and later washed in a sieve. The remaining particles were dried and later analysed. From the remains in each dropping the types of food items were identified as well as possible. Then, the food category making up the greatest volume of the dropping was determined. Remains of mammals were identified with the aid of material in the Nairobi National Museum and with a collection of hair samples from species in the field. Because identification of species was often uncertain, only four categories of mammals were distinguished; a. Big game, such as zebra, wildebeest, etc., which jackals would not have killed; b. Small game of the size of hares up to adult Thomson's gazelles, which could have been killed by the jackals; c. Small mammals of the size of rats and mice; d. Unidentified mammals, i.e. remains of mammalian origin, which could not be put into one of the former categories unequivocally. Identification of invertebrate remains was carried out with the kind help of Mr. M. CLIFTON from the National Museum in Nairobi.

3 Diet

The qualitative list of food items (Table 1) revealed that in the Serengeti jackals ate the same types of food, as in other areas (VAN DER MERWE 1953; GRAFTON 1965; BOTHMA 1966, 1971; VAN LAWICK 1970; ROWE-ROWE 1976).

In table 2 the results of faecal analysis are summarized. For both jackal species, collection dates of faecal samples were not equally distributed over the year, and the majority of samples of the two species were taken at different times of the year. Furthermore, the samples were predominantly collected in the normal breeding area of the species, which were different for *C. mesomelas* and *C. aureus*. This renders

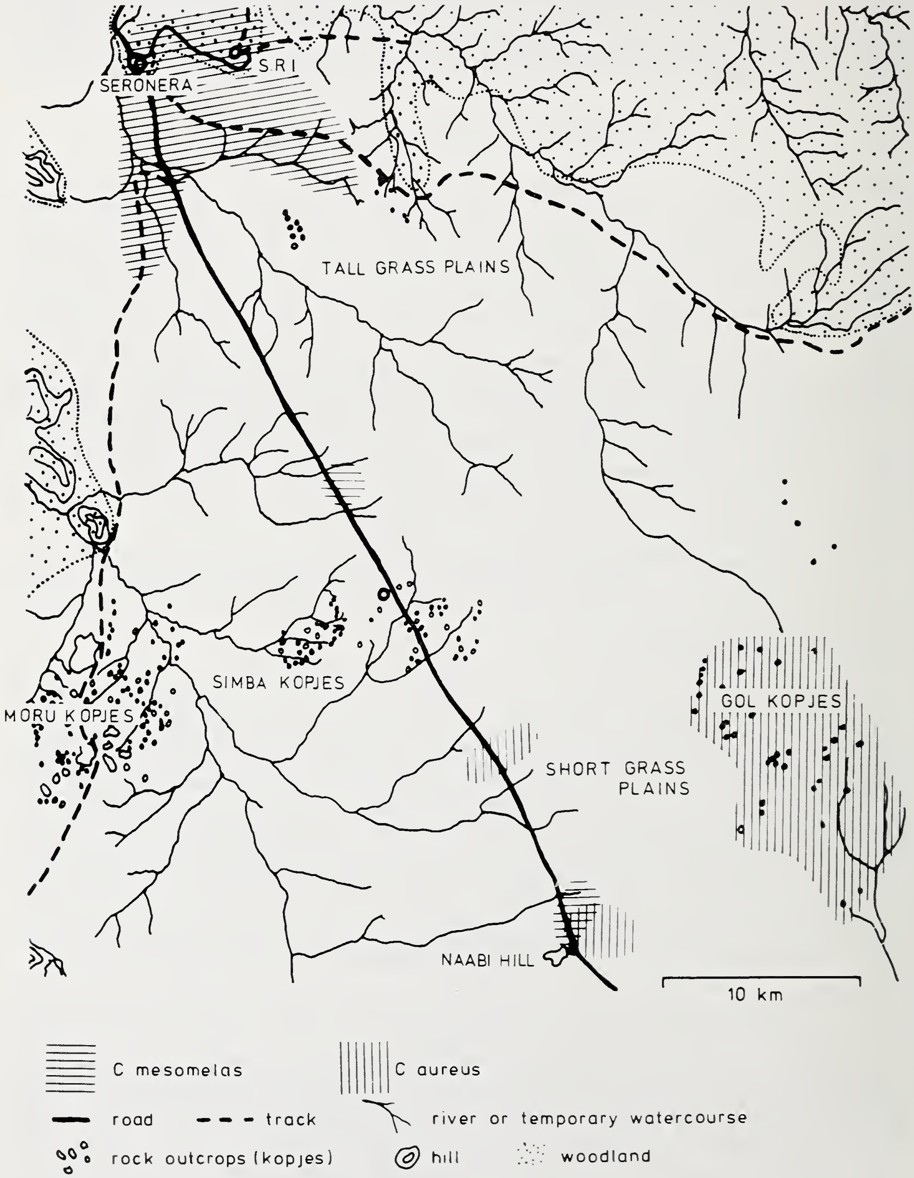

Fig. 1. Study areas of *Canis mesomelas* and *C. aureus* on the Serengeti plains

Table 1

Qualitative list of food items of *C. mesomelas* and *C. aureus* in the Serengeti, compiled from direct observation, stomach contents and faecal analysis

(+ = eaten; s = scavenged; h = hunted)

	Food category	Species or item	C. mes.	C. aur.
Vertebrata	Big game	Zebra, Equus burchelli	+ s	+ s
		Wildebeest, Connochaetes taurinus	+ s	+ s
		Grant's gazelle, Gazella granti		+ s
		Ungulate placenta	+	
	Small game	Thomson's gazelle, Gazella thomsoni ad.	+ s h	+ s
		" " , " " fawn	+ h	+ h
		Grant's gazelle, Gazella granti, fawn	+ h	+ h
		Warthog, Phacocoerus aethiopicus, young	+	
		Spring hare, Pedetes capensis		+ h
		Cape hare, Lepus capensis	+ h	+
		Dwarf mongoose, Helogale parvula	+ h	
	Small mammals	Unidentified rodents	+	+ h
	Birds	Hildebrandt's starling, Spreo hildebrandti	+	
		Caspian plover, Charadrius asiaticus		+ h
		Unidentified bird	+	+
		eggs of Crowned plover, Stephanibyx coronatus		+
		eggs of Senegal plover, Stephanibyx lugubris		+
	Amphibia	Unidentified frog	+	
Invertebrata	Diplopoda	Unidentified species	+	
	Chilopoda	Centipedes		+
	Insecta (Coleoptera)	Coprinae (Dung beetles)	+	+
		" (Dung beetles), larvae	+	+
		Melolonthinae	+	+
		Carabidae	+	
		Buprestidae	+	
		other unidentified beetles	+	+
	Insecta (Isoptera)	Termites, Hodotermes mossambicus	+	
		Unidentified termites	+	
	Insecta (Orthoptera)	Gryllidae (Crickets)	+	+
		Blattidae (Cockroaches)		+
		Tettigonidae (Grasshoppers)	+	
		Acrididae (Grasshoppers)	+	+
	Insecta (Diptera)	Muscidae, pupa		+
	Arachnida	Unidentified spiders	+	+
Vegetable matter		Fruits of Balanites aegyptica	+	
		Grass	+	+
		Unidentified seeds	+	+
Other items		Sand and grit	+	+
		Paper, cardboard, cottonwool	+	+

comparisons between seasons and between the two species problematical. The data are nevertheless presented, because they reveal some interesting aspects of the jackals' diet.

Mammals, arthropods and vegetable food were the main food categories in both species. The data seem to indicate that mammals were more important as food for *C. mesomelas* than for *C. aureus*. This agrees with WYMAN's (1967) findings. In both species small game remains were present in most of the samples containing mammalian remains. Remains of scavenged big game were less frequent, indicating that jackals predominantly hunted their mammalian food themselves. *Balanites* fruits were not available to the *C. aureus* in the study areas and human refuse, indicated by paper and cardboard in the faeces, was also much more available to the *C. mesomelas* living in the inhabited Seronera area.

A comparison between wet and dry season samples in *C. mesomelas* indicates that this species eats more arthropod food in the wet season and more mammalian food in the dry season, a tendency which is not present in the *C. aureus* data.

Table 2

% of faecal samples containing remains of a given food category

In brackets: % of samples, in which remains of a given food category made up the greatest volume. (n = number of samples)

		Mammals				Birds	Arthropods		Vegetable matter		Paper
		total	Big game	Small game	Small mammals		total	Beetles	total	Balanites seeds	Cardboard
Canis mesomelas	all samples n = 45	82 (69)	11	71	11	7 (o)	38 (7)	33	87 (18)	29	7 (7)
Canis mesomelas	dry season May – Oct. n = 19	1oo (79)	16	79	21	16 (o)	o (o)	o	95 (11)	16	11 (11)
Canis mesomelas	wet season Nov. – Apr. n = 26	69 (62)	8	65	4	o (o)	65 (12)	58	81 (23)	39	4 (4)
Canis aureus	all samples n = 37	57 (3o)	5	35	22	3 (o)	1oo (65)	97	51 (5)		3 (o)
Canis aureus	dry season May – Oct. n = 12	58 (42)	17	33	25	o (o)	1oo (58)	1oo	5o (o)		o (o)
Canis aureus	wet season Nov. – Apr. n = 25	56 (24)	o	36	2o	4 (o)	1oo (68)	96	52 (8)		4 (o)

4 Foraging

4.1 Gathering

Gathering can be defined as a type of foraging behaviour, in which food items localized by random or non-random search need only be consumed. Food normally obtained in this way consists of relatively small items that do not run away and can hardly be stolen.

When ripe *Balanites* fruits were available, *C. mesomelas* systematically visited *Balanites* trees on their foraging tours. A *C. aureus* was repeatedly seen searching areas, where plovers had previously given alarm calls. It was presumably looking for eggs. *C. mesomelas* were regularly seen visiting the vicinity of houses for refuse at night. Remote refuse pits were searched even during the day. Jackals often were observed systematically visiting the dung heaps of large ungulates and searching for dung beetles. During one night a *C. aureus* was seen eating up to 37 beetles per 30 mins. It consumed predominantly beetles during the night. Dung beetle larvae developing within dungballs under ground were dug up and eaten by jackals of both species. Kruuk (1972) and Leakey (1969) presumed that jackals localize these larvae by listening to their gnawing sounds. Searching jackals sometimes found pieces of meat in grass tufts under bushes or fallen trees. In most cases it remained uncertainly whether a particular piece stemmed from the jackal's own previous meal or from that of some other animal.

4.2 Hunting

The term hunting is used here to designate means of acquiring food items, which are able either to escape or to fight back. Jackals usually jumped after flying dung beetles or clumsily fluttering birds at night and tried to knock them down with their fore paws. They also caught mice, rats, frogs, lizards, etc. Species of such small size were hunted and eaten alone. If the prey was of the size of a Cape hare or bigger, two adult jackals often concentrated their hunting efforts on the same object.

4.2.1 Hunting Cape hares and Spring hares

When searching in bushes or high grass jackals sometimes disturbed resting Cape hares, which suddenly ran away. *C. mesomelas* tried to catch these Cape hares in 8 out of 9 instances. In most cases the hare ran faster than the jackals, or it disappeared into a hole. In 3 of the 8 hunts the hare was chased by a single jackal and only once was the chase successful. The remaining 5 hunts were carried out by 2 jackals simultaneously. Still only one of them was successful. *C. aureus* hunted 7 of 11 encountered Cape hares. None of the hunts was successful. Two single *C. aureus* were seen chasing Spring hares at night on 5 occasions. One was successful twice while the other was unsuccessful three times. For both jackal species data are not sufficient to demonstrate whether success rates of pair and individual hunts differ.

Cape hares seemed to have prefered resting places and holes, and relatively fixed escape routes, all of which jackals might have been able to learn on unsuccessful hunts. During extended observations, I had the impression that one pair of *C. mesomelas* systematically visited and searched the resting place of a hare, and that co-operation as well as their knowledge of the hare's escape route made their hunt successful:

13. 8. 1973: A pair of *C. mesomelas* was foraging in relatively high grass. The ♂ flushed a Cape hare and ran behind it for a few meters. Then both jackals left the hare's course and ran parallel to it, losing sight of the hare. Later the hare appeared again, turning in the direction of the jackals. They almost intercepted the hare's course, but it ran faster and reached a termite mound, where it disappeared into a hole. The jackals spent some minutes sniffing at the entrance of the hole, before they trotted on.

21. 8. 1973: The same pair was foraging in the same area. They trotted towards the high grass area where the ♂ had encountered the hare the last time. The ♀ flushed a hare almost in the same place. It escaped in the same direction as last time with the female jackal close behind. The male jackal ran approximately 15 m parallel to them, watching and almost overtaking them. The hare ran very fast, turning towards the male jackal and the termite mound. It managed to cross in front of the jackal. As it reached the termite mound the jackal was only 1 m behind, so the hare could not stop to enter the hole. It ran past the hole with both jackals in pursuit. They all disappeared behind an elevation. — When I saw them again the ♂ was carrying the dead hare, followed by the ♀.

This successful hunt was at least the second attempt to catch a hare, which most probably was the same individual.

4.2.2 Hunting gazelle fawns

C. mesomelas were observed hunting a Grant's gazelle fawn once and Thomson's gazelle fawns 18 times. *C. aureus* were seen hunting Grant's gazelle fawn twice and on 12 occasions Thomson's gazelle fawns. The fawns were regularly left by their mothers in patches of tall grass or on the short grass plains between small shrubs or broad-leaved herbs. There they crouched and took flight only when closely approached.

When a jackal searched for a gazelle fawn, it trotted straight towards an aggregation of female Thomson's gazelles with its head held high. The ♂ of a pair normally took the more active part. Upon arrival it very actively zigzaged in the area, searching the ground especially in patches of high grass or shrubs. When it found nothing it scanned the horizon and then trotted straight towards another group of gazelle ♀♀ where the searching of the ground was repeated. This strategy was most often observed in *C. aureus* on the open plains.

C. mesomelas pairs were often seen systematically searching patches of tall grass. When a fawn jumped up in front of the searching jackals, it was always captured as the jackals could secure it undisturbed by the fawn's mother. Such „pick-ups" could easily be distinguished from chases. Chases usually resulted when a fawn was found near its mother, and could run away because the mother defended it, or when the jackal spotted a fawn from a distance of up to 200 m and started running towards it. Chases were not always successful. In *C. mesomelas* 13 out of 17 resulted in a kill, and in *C. aureus* only 6 out of 13.

When chased by a jackal young fawns tended to run in a circle; this was to their disadvantage because the second jackal often had time to join the hunt even at the height of the chase. Older fawns normally escaped in a straight line, which made it more difficult for the second jackal to catch up and take part in the chase and killing. During the chase the adult gazelle normally tried to zigzag between the jackal and the fawn, disturbing the jackal's course. When the fawn had been pulled down, it's mother attacked the predator with her horns. The hunter usually gave way and was vigorously pursued, thus having little opportunity to concentrate on the fawn. Sometimes more than one female gazelle attacked the jackals.

The jackals of both species had no special killing bite for gazelle fawns. They opened the body cavity of the quarry as soon as possible, usually starting at the groin and disembowelling it. Thomson's gazelle fawns were usually dead in about half a minute.

A single jackal had great difficulties holding a fawn on the ground, when it was constantly attacked by the fawn's mother. When 2 jackals were taking part in the hunt, one was chased by the gazelle, while the other could concentrate on the fawn. One would expect therefore that hunting success rates are higher in pair hunts than in individual hunts.

Table 3

C. mesomelas			C. aureus		
No. of hunting jackals	No. of defending gazelles	Kills	No. of hunting jackals	No. of defending gazelles	Kills
3	ca. 1o	o	2	2	1
3	1	1	2	2	1
2	2	o	2	1	1
2	1	1	2	1	1
2	1	1	2	o	1
2	1	1	1	2	o
2	o	1	1	1	1
2	o	1	1	1	o
1	1	1	1	1	o
1	1	o	1	1	o
1	1	1	1	o	o
1	o	1	1	o	o

In table 3 the gazelle fawn chases are summarized, in which the number of hunting jackals and the number of defending adult gazelles were known. Hunting success rates, average number of defending gazelles per hunting jackal and the ratio between single hunts and pair or group hunts did not significantly differ between the two jackal species.

Table 4

		Kendall rank correlation coefficient τ					
		C. mesomelas (n = 12)		C. aureus (n = 12)		C. mes. + C. aur. (n = 24)	
Variable 1	Variable 2	τ	p*	τ	p*	τ	p*
No. of hunting jackals	No. of defending adult gazelles	0.65	< 0.004	0.78	< 0.0005	0.65	< 0.00001
No. of hunting jackals	Hunting success of jackals	0.15	> 0.5	0.99	< 0.00001	0.52	< 0.0005
No. of defending adult gazelles	Hunting success of jackals	−0.45	< 0.05	0.55	< 0.02	0.14	< 0.4
No. of defending gazelles per jackal	Hunting success of jackals	−0.50	< 0.03	0.15	> 0.5	−0.15	< 0.3

*p – values are two-tailed ; n = number of hunts

Table 4 shows the relationships between various aspects of the fawn hunts. In *C. aureus* the Kendall rank correlation coefficient (Siegel 1956) revealed that pair hunting was significantly more successful than individual hunting. This effect was not detectable in the *C. mesomelas* data, where success rates in individual and pair hunts were equal.

When more adult gazelles per jackal were defending the fawn, the *C. mesomelas* were significantly less successful in the hunt. This was not true for *C. aureus*. In this species a positive correlation between number of defending gazelles and success of jackals was found, which was probably due to the highly positive correlation between numbers of jackals and adult gazelles involved in the fawn chases.

In both species the Kendall partial rank correlation coefficients[2] revealed a positive relationship of jackal numbers and a negative relationship of adult gazelles' numbers with the hunting success of the jackals. The partial correlation between numbers of jackals and numbers of defending gazelles was positive.

Although different relationships were found significant in the two jackal species, none of the species differences were significant. Some of the variation in the data was probably due to factors which had not been recorded in the field such as the distance of the fawn at the onset of the chase, cover available to the fawn and minor age differences between the fawns.

Since Wyman (1967) used combined data for *C. mesomelas* and *C. aureus*, the results of the pooled data (24 hunts) of both species in this study are given in table 4 for comparison.

4.2.3 Hunting adult gazelles

Although the jackals of the Serengeti might be able to subsist on insects, fruits and small rodents alone (Schaller 1972) and their biggest regular prey animals are gazelle fawns, jackals have sometimes been observed killing larger prey animals. I occasionally saw *C. mesomelas* ♂♂ rush suddenly towards adult female Thomson's gazelles. All such gazelles leisurely stotted away, and the jackals did not pursue them further than about 20 m. In this way jackals might have been testing whether a gazelle was sick and therefore easy prey.

While I never observed jackals attacking adult Grant's gazelles, 4 serious attempts

[2] No test of significance for the Kendall partial rank correlation coefficient is available (Siegel 1956).

on grown-up Thomson's gazelles (2 by *C. mesomelas* and 2 by *C. aureus)* were recorded. In the only successful one a *C. mesomelas* ♂ killed an adult male Thomson's gazelle, which was probably sick, because it seemed exhausted after a slow chase of only 300 m.

Other authors have made similar observations, showing that jackals of both species are able to successfully hunt bigger prey than gazelle fawns (VAN DER MERWE 1953; VAN LAWICK 1970; KRUUK 1972; SCHALLER 1972; SLEICHER 1973).

4.3 Scavenging

Searching for refuse near human habitations is sometimes called scavenging, although it cannot really be distinguished from gathering small food items in other areas. Typical scavenging is eating from a sizeable prey, which had been killed by disease, another predator, or in an accident. The essence of this rather vague term seems to be that a scavenger eats prey, which would otherwise have required a considerable hunting or searching effort.

The jackals of the Serengeti were often seen at refuse pits and at night between houses where they occasionally found small food items. Carcasses of various animals were also sometimes available to the jackals. Occasionally I encountered several dead but untouched adult Thomson's gazelles scattered on the open plains. They had probably died of some disease. Cape hares and gazelles were often killed by cars at night.

Jackals were regularly encountered near kills of larger predators. They were attracted from great distances to places where vultures alighted or were assembled. Giggling sounds of spotted hyaenas quarreling over a kill equally attracted jackals from many hundred of meters. Near a lion kill jackals normally waited until the lions walked off, but a bold jackal sometimes obtained a piece of meat even earlier by a fast dash at the carcass. Spotted hyaenas scattered pieces of their kills much more widely than lions or cheetahs did, and thus jackals often found a piece of meat in the vicinity of a hyaena kill without having to advance to the carcass.

WYMAN (1967) tried to estimate the relative importance of scavenging for jackals. From faecal analysis he estimated the percentage of food obtained by scavenging as about 3 % for both jackal species on the Serengeti plains. Although he probably underestimated the importance of scavenging, as he regarded adult Thomson's gazelles as not being scavenged, the fact remains that in the Serengeti jackals live mainly on self-caught invertebrate and vertebrate food.

5 Food competition

In the Serengeti, where prey abundance is hardly affected by predation (KRUUK 1972), most competitive interactions between predators were observed in the presence of carcasses. Especially where predators are numerous, as in this area, strategies allowing scavenging another's prey as well as strategies against being robbed by others can be expected to be favoured by natural selection.

5.1 Observations of competitive interactions

5.1.1 Jackals versus other meat eaters

Access to a carcass occupied by others and success in defending prey against scavengers largely depends upon the animal's relative physical strength. In terms of this variable both jackal species seemed to be inferior to lions, cheetahs, and African wild dogs, with whom they often competed for food.

At big carcasses, jackals were regularly found in competition with marabou storks, vultures, or eagles. When they found a dead animal already occupied by many vultures, they rushed towards them with their heads low, ears flattened and tails whipping from side to side. In this manner they could usually scare away all vulture species from the carcass for some time. However, I saw them give up eating after too many vultures had aggregated. They fed again, when the vultures had been scared away by hyaenas. Small game like gazelle fawns or hares, on the other hand, rarely attracted carnivorous birds, and when birds were present, they never numbered more than four.

In the Serengeti, the most important robber of the jackals' prey was the spotted hyaena. This species was very common in the area and it often appeared soon after the jackals had caught a sizeable prey. I saw *C. mesomelas* capturing hares or gazelle fawns 17 times. They lost the entire prey to a hyaena 4 times, and about half of it twice. In one case the outcome was uncertain. In the remainder of instances, they were able to eat their prey entirely, and once a jackal, chased by a hyaena, successfully escaped with a small piece of meat in its mouth. *C. mesomelas* lost in effect 5 of their 17 self-caught prey, which was about 30%. This is even more than the 3% of food, which according to Wyman (1967) they normally gain by scavenging. The competitive pressure on *C. aureus* might not be so strong. Of 9 observed kills only one entire gazelle fawn (11%) was lost to hyaenas.

Similar instances of jackals being robbed of their prey by spotted hyaenas have been reported by Kruuk (1972).

C. mesomelas that I could follow on feeding trips at a distance of 15—30 m, were reluctant to let me drive closer than about 40 m after they had killed a fawn or a hare. When I did, they tried to run away with the prey. *C. aureus* were also much shyer with regard to my car after killing a gazelle fawn. The increased flight distance seemed to reflect the jackals' awareness of a potentially stronger competitor. It indicates the existence of competitive pressure, which need be avoided immediately after making a kill.

5.1.2 Canis mesomelas versus Canis aureus and inter-group competition

In some instances *C. mesomelas* drove *C. aureus* off a carcass, in others *C. aureus* seemed to dominate over *C. mesomelas* in similar situations. In the Ngorongoro crater Wyman (1967) had often seen both jackal species feeding side by side on kills. Thus, from the few observations no conclusions about interspecific dominance relationships between the two jackal species can be drawn.

When different pairs or family groups of *C. mesomelas* met around a carcass, I regularly observed agonistic encounters such as threats and short chases between them. Different pairs or groups of *C. aureus* seemed to meet less often at carcasses than *C. mesomelas* groups. Several times I saw a pair of *C. aureus* eating a carcass while two others watched them from a distance of 200—300 m without approaching. I never observed such situations in *C. mesomelas*.

5.1.3 Caches being plundered

After the jackals had eaten their fill, the remains were stored in holes or under bushes. But these caches were frequently plundered by other animals. Tawny eagels *(Aquila rapax)* often sat watching a jackal hide a piece of meat, and flew over to it after the jackal had left. I saw jackals returning to their cache many times to chase off such eagles. Once 5 Tawny eagles were seen quarreling over the leg of a gazelle fawn, which a *C. aureus* had hidden in a hole 80 min beforehand. Tawny eagles seemed to plunder jackal caches fairly systematically. There are other species such as spotted hyaenas, porcupines, mongooses, small cats or even other jackals, which might eventually find caches and eat the contents (see also VAN LAWICK 1970).

5.2 Strategies against being robbed

There are some aspects of the jackals' behaviour in the presence of their prey, which appear to be adaptations against being robbed by stronger carnivores.

5.2.1 Dividing up prey before eating

After an individual or a pair of jackals secured prey such as a gazelle fawn or a hare, one or both divided the animal into a front and a rear piece. The pieces were eaten alone by the individuals at distances of 5 to 40 m. Single jackals, having cut up the prey into two pieces, would regularly cache the first piece and come back and eat the other, or also cache it. The advantage of this behaviour became obvious when I watched two *C. mesomelas* eating the two pieces of a Thomson's gazelle fawn, while being 40 m apart. A hyaena approached and robbed the female jackal of her piece. In the meantime the ♂ quietly sneaked away with his part of the prey. Later the pair shared the male's piece. Had the prey not been divided up, the hyaena would have taken the lot.

I never observed a jackal actively defending its prey against a hyaena, and I never saw hyaenas being mobbed (i.e. barked at with biting intentions) after stealing the jackals' prey. In both species, vigorous and successful attacking of hyaenas was only observed in the defence of the den with cubs.

5.2.2 Fast eating

The sooner the food reaches the stomach the smaller are the chances of losing it to others. This might be the reason why jackals and other meat-eaters, such as vultures, spotted hyaenas, or African wild dogs, so hectically devour big carcasses. Jackals swallowed fist-sized pieces of meat without chewing them. However, when they ate small food items like beetles, mice or small single pieces of meat, which could hardly be stolen, they took time to chew, and the feeding movements were much slower.

5.2.3 Caching food

Jackals of both species cache food in the same manner as many other canids (see MACDONALD 1976). Normally pieces to be cached were carried in the mouth. I saw a *C. mesomelas* cache regurgitated food once only.

From his observations, WYMAN (1967) got the impression that the majority of jackal caches were recovered within 24 h. I once observed a *C. mesomelas* retrieving a cached piece of meat after 13 h, and a *C. aureus* dug out some meat, which he had cached about 6 h previously.

As a rule, meat was not normally cached where it could most easily be retrieved (e. g. near resting places), but where it could rapidly be cached. This was in the vicinity of a large carcass or where the self-caught prey was eaten. When a jackal was carrying a piece of meat, it could be detected from a distance of 300—500 m with the aid of binoculars. Spotted hyaenas also seemed to be able to see it from a great distance. They regularly approached and chased such a jackal trying to steal its food. It therefore seems advantageous for jackals in the Serengeti to cache food close to the place where it was obtained. However, I saw *C. aureus* carrying heads of gazelle fawns to the young over hundreds of meters several times. Maybe they did it, when they could see that there were no hyaenas around, which was possible on the open short grass plains.

5.2.4 Hunting in pairs for fast exploitation of prey

The more group members, which take part in the exploitation of a prey, the sooner the prey is consumed, and the smaller the chances of losing some of it to stronger competitors. Thus hunting in pairs instead of singly can not only increase hunting success on bigger prey, it can also reduce losses of prey to competitors like hyaenas.

6 Discussion

When all observed hare and gazelle fawn hunts are analysed together (25 chases in each jackal species), *C. mesomelas* was successful in 60 % and *C. aureus* in 32 %. Comparing these rates with the overall hunting success rates of lions (26 %, after Schaller 1972), spotted hyaenas (35 %, after Kruuk 1972), cheetahs (70 %, after Schaller 1972) and wild dogs (70—86 %, Schaller 1972; Estes and Goddard 1967), one recognizes *C. mesomelas* as a highly successful hunter, while *C. aureus* is only moderately successful. This might be one reason, why the latter seemed to rely more on small invertebrate food (Table 2, and Wyman 1967).

Single *C. aureus* were successful in 14.3 % of their gazelle fawn chases, while pairs were always successful. *C. mesomelas* killed the fawn in 75 % of their chases under both conditions (see table 3). Wyman (1967) gave hunting success rates for both species together as 16 % for individual hunts and 67 % for pair hunts. When the data for both species in this study are pooled the success rates are 36.4 % for individual hunts and 84.6 % for jackals hunting in groups of 2 or 3. The increase in hunting success is more than proportional to the number of hunters and thus reflects the effect of actual co-operation of members of the hunting party (see also Kruuk 1975).

In both jackal species a significant positive correlation was found between the numbers of jackals and adult gazelles actively involved in a fawn hunt. This could reflect an anti-predator behaviour of gazelle ♀♀: that they tend to defend a fawn in greater numbers when more jackals hunt it. But behavioural observations favouring this idea are not available, and it therefore remains only one of several possible interpretations of the correlation.

Jackals hunting adult gazelles in packs of more than two individuals were seldom observed. There are several possible reasons for the rareness of pack hunting in jackals in areas where other carnivores (e.g. wild dogs) successfully hunt in packs:

1. Success rates of jackal packs which are not known, might be too low because adult gazelles run much faster than short-legged jackals. Sick gazelles, on the other hand, which are easier to catch, might be too rare to justify regular pack formation. Furthermore, specializing in capturing healthy adult gazelles might lead to increased body size in jackals, which could cause an inability to subsist on small food items alone. This might reduce other advantages of the jackals' present ecology, and render pack hunting inefficient.
2. There might be unknown factors of a social nature counteracting pack hunting, even though the jackals seemed to have the social potential to form packs: a. The various hunting groups of 3—7 *C. aureus* observed by van Lawick (1970) most probably consisted of pairs with their grown-up offspring. b. Yearlings which were probably the offspring of the former season, were often seen around the dens

of adult pairs with small cubs. However, these yearlings were never observed joining the adult pair on a foraging trip, even when they left the den at the same time (LAMPRECHT in prep.).

3. An important factor, which could limit hunting groups size in jackals, as well as increase it in other carnivores, is competition over carcasses. As argued elsewhere (LAMPRECHT 1978), the jackals might pursue a strategy of inconspicuousness, by hunting small game in small groups, to avoid losing their prey to physically stronger scavengers, especially spotted hyaenas.

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Zusammenfassung

Nahrung, Nahrungserwerb und interspezifische Beutekonkurrenz von Schakalen des Serengeti National Parks, Ost-Afrika

Untersucht wurden Nahrungszusammensetzung, Methoden des Nahrungserwerbs sowie Beutekonkurrenz mit anderen Fleischfressern bei Gold- und Schabrackenschakalen (*Canis aureus* L. und *C. mesomelas* Schreber).

Beide Arten fraßen Arthropoden und Pflanzenteile, jagten Mäuse, Kaphasen, Springhasen, Gazellenkitze und in einigen wenigen Fällen adulte Thomson Gazellen. Thomson Gazellenkitze waren die häufigsten größeren Beutetiere beider Schakalarten. Auf der Kitzjagd waren die Paare erfolgreicher als Einzeljäger (signifikant für *C. aureus*). Der Jagderfolg war um so geringer, je mehr adulte Gazellen-♀♀ das attackierte Kitz verteidigten (signifikant für *C. mesomelas*). Bei der Jagd auf Kitze und Hasen waren *C. mesomelas* insgesamt in 60%, *C. aureus* in 32% der Versuche erfolgreich. Beide Arten verloren einen beträchtlichen Teil ihrer eigenen Beute (*C. mesomelas* bis zu 30%) an räuberische Fleckenhyänen. Außerdem wurden ihre Futterverstecke oft von Raubvögeln und anderen Fleischfressern geplündert. Die folgenden Verhaltensweisen dürfen der Verminderung von Beuteverlusten an räuberische Konkurrenten dienen: (a) Das Teilen der Beute unmittelbar nach dem Fang, verbunden mit dem Fressen der Stücke an verschiedenen Plätzen, (b) rasches Fressen, (c) Futterverstecken in der Nähe des Kadavers, und (d) Jagen in Paaren zur rascheren Verwertung der Beute.

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Why deer shed antlers[1]

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Abstract

This paper discusses hypotheses explaining the shedding of antlers and horn-sheaths in deer and *Antilocapra* respectively. A number of earlier hypotheses pertaining to antler-shedding are reviewed critically; the views that antlers evolved to store excess minerals or hormones or shed excess heat are found wanting.

A theory explaining the shedding of hornlike organs must account for the origin of this

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