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Space and resource use by brown hyenas *Hyaena brunnea* in the Namib Desert

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(With 2 figures in the text)

Two clans of brown hyenas were studied on the arid chilly Namib Desert coast where very large seal colonies are present. Carcasses from seals were abundant during summer and autumn following the seal pupping season, and scarce in winter and spring. Hyenas fed predominantly on carcasses. Members of one clan of three hyenas obtained most of their food along 3 km of coastline adjacent to the seal colonies. The other clan of nine individuals obtained food from an area along 6 km of coastline north of the seal colonies. Although carcasses were usually scavenged, seal pups were seen to be killed on occasions. Time spent foraging was not affected by carcass availability. Territories of the two clans overlapped and individual home-range size varied from 31·9 to 220 km^2. Food availability apparently had no influence on foraging activities but the dispersal of food affected territory and group sizes. Over abundance of food results in the maintenance of territories extending beyond the distribution of food. The shape and area of these territories may result from the cultural inheritance of space.

Contents

Introduction

Brown hyenas *Hyaena brunnea* are solitary scavengers occurring through much of the southern African subregion. They feed opportunistically on a variety of vertebrates (Skinner, 1976; Mills, 1978; Owens & Owens, 1978). Analyses of scats and food remains have shown that brown hyenas living in the vicinity of Cape fur seal *Arctocephalus pusillus* colonies along the coast of the Namib Desert feed largely on these seals (Skinner & van Aarde, 1981, 1991). No published information, however, is available on their foraging behaviour or habitat utilization in the Namib Desert.

Brown hyenas live in small groups (Mills, 1982) which in the southern Kalahari vary from four to 14 usually related members (Mills, 1984). Each group has a territory with little overlap between neighbouring territories (Mills, 1982) throughout which scent marks are deposited, particularly along the boundaries (Mills, Gorman & Mills, 1980). Territory size of these groups is known to be affected by food dispersal, while group size depends on the quality of available food within the group's territory (Mills, 1982, 1990).

In the present paper, using direct observations, we examine resource utilization and territoriality, as well as food acquisition of some members of two distinct clans of brown hyenas. One of these clans lived near the inhabited coastal town of Luderitz, and the other, adjoining clan in an area uninhabited by humans but including two Cape fur seal colonies on the coast of the Namib Desert. Apparent differences in the resource base of these two clans thus provide an opportunity to quantify the influence of resource characteristics on aspects of the behavioural ecology of these brown hyenas and to relate our observations to the Resource Dispersion Hypothesis of Macdonald (1983) and Carr & Macdonald (1986).

Study area

The study was conducted in an area approximately 400 km^2 along a 50 km stretch of the coastline of the central Namib Desert, from Luderitz (26°39′S, 15°09′E) in the north to Elizabeth Bay (26°50′S, 15°15′E) in the south (Fig. 1). At the time of the study, Luderitz was inhabited by some 3500 residents involved in industry and commerce in the town itself. The town is situated in an unrestricted enclave of about 70 km^2 surrounded by Diamond Area No. 1, which is a highly restricted zone running along the coast and about 100 km to the interior. The rest of the study area and an area of approximately 30 000 km^2 surrounding Luderitz is uninhabited. Remnants of earlier mining activities exist in the form of ruined abandoned towns and machinery on several sites throughout the study area.

This cool coastal desert ecosystem is extremely dry, with an average annual rainfall of less than 100 mm (Besler, 1972), and is maintained by the effects of the cold Benguela current (Ward, Seely & Lancaster, 1983). Temperatures frequently decline below zero but the mean annual temperature is 15 °C (Skinner, van Aarde & van Jaarsveld, 1984). Relatively low temperatures and the high wind speeds along the coast (median annual windspeed ≈19 m/sec) result in mammals living here being exposed to extremely cold environmental conditions (Skinner *et al.*, 1984). No permanent stands of fresh water are available but hyenas were occasionally seen drinking water leaking from a reservoir close to Luderitz.

Succulent xerophytic vegetation is sparse and occurs mainly in and along drainage channels bisecting wide, wind-eroded gravel plains that separate low, isolated hills which comprise metamorphosed sediments of the Bogenfels Formation. In places sand has been blown into dunes tens of metres in height. The convoluted coastline is rocky, but the larger bays have long sandy beaches.

Flocks of flamingos *Phoenicopterus* spp. and cormorants *Phalacrocorax* spp. roost along the coast but the density and diversity of terrestrial mammals are very low. Mammals other than brown hyenas seen here included: 27 to 30 black-backed jackals *Canis mesomelas*, a few feral and free-ranging dogs *Canis familiaris*, free-ranging domestic cats *Felis catus*, a few springbok *Antidorcas marsupialis*, and occasional steenbok *Raphicerus campestris*, gemsbok *Oryx gazella*, hares *Lepus capensis*, rock rabbits *Pronolagus* spp., gerbils *Desmodillus* spp. and Cape porcupines *Hystrix africaeaustralis*.

Apart from seabirds and seals, other vertebrates provide a sparse food supply. The study area encompassed two Cape fur seal colonies with individuals of varying ages and sex occurring

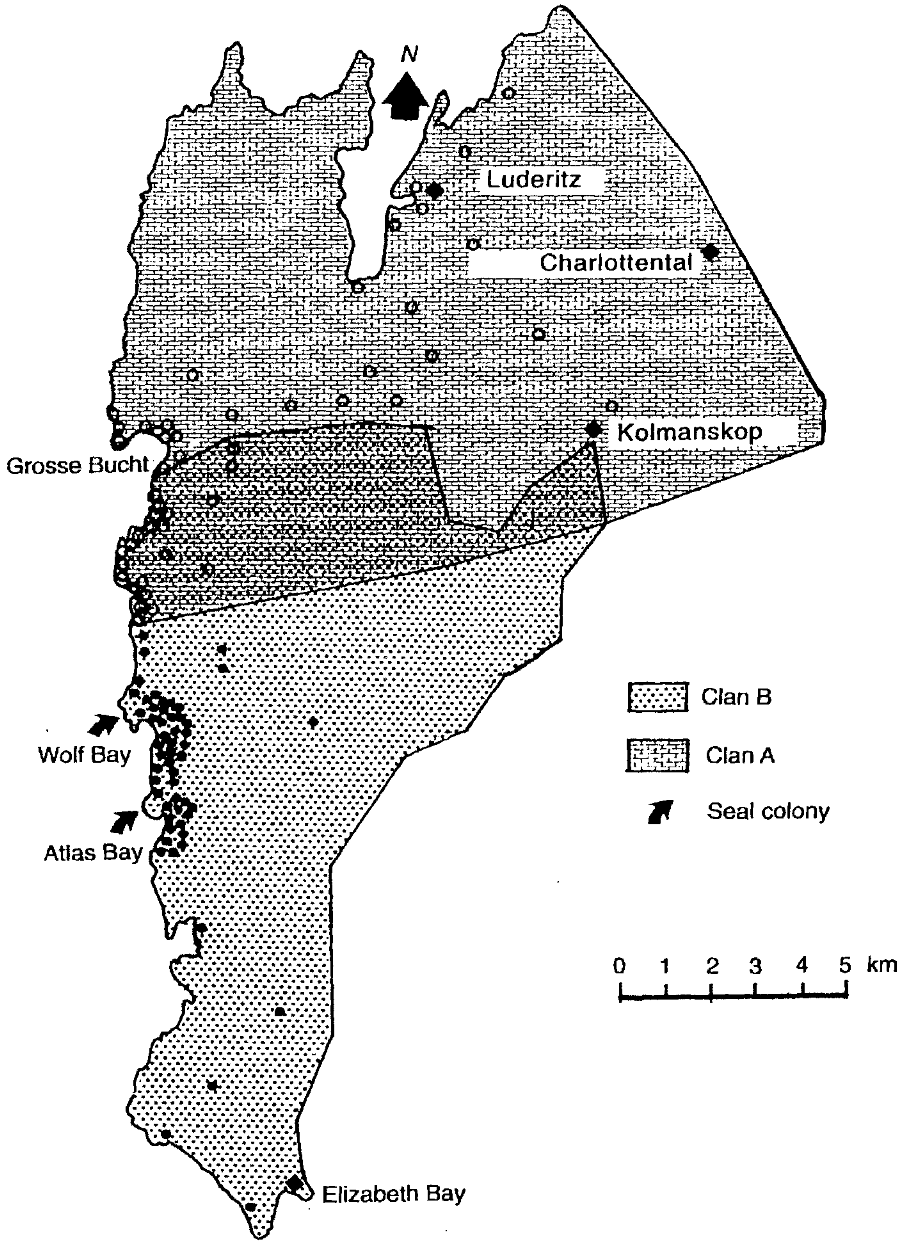

FIG. 1. Territory boundaries of two clans of brown hyenas inhabiting the coastal area between Luderitz (26°39′S, 15°09′E) and Elizabeth Bay (26°50′S, 15°15′E): abandoned mining ruins (◆); feeding sites (n = 142) of Clan A (○) and feeding sites (n = 63) of Clan B (●). The location of the seal colonies is indicated by arrows.

throughout the year in large numbers. Prior to World War II, no seals bred here (Best, 1973) and only young seals concentrated in these bays (Wolf and Atlas Bays, Fig. 1) before 1948 (Rand, 1959), however, by 1982 the population comprised some 453 000 individuals (J. David, pers. comm.). Seal carcasses (mainly those of pups and under-yearlings) originating from these colonies and from colonies on islands along the coast wash up along most of the coastline and, together with occasional carcasses of dolphins, whales and seabirds, are a source of food for brown hyenas and black-backed jackals.

Materials and methods

Information on aspects of food acquisition was obtained through direct observations on 5 hyenas fitted with radio-collars (AVM Instrument Company Ltd., California, USA) on to which green glowing beta lights (Saunders Roe Development Co. Ltd., Hayes, UK) were fitted as described by Mills (1978). These individuals were members of 2 distinct clans, with Clan A centring its activities in the vicinity of Luderitz and Clan B centring its activities on the seal colonies at Wolf and Atlas Bays. Initially, observations were made at night from a 4-wheel drive vehicle by using a hand-held spotlight with a red filter or a night vision scope (Bostock Ltd., Cambridge, UK). After about 4 weeks, the hyenas became habituated to our presence and could be observed in the headlights of the vehicle at distances of 10–25 m.

Individual hyenas were located through triangulation before sunset and followed at distances of 25–40 m in a 4 × 4 vehicle for as long as possible while roaming through their home ranges. The distances they travelled were recorded from the vehicle's odometer and the routes they followed were plotted on to aerial photographs on a scale of 1 : 52800. The location, time and duration of all feeding and marking events that occurred were recorded on a tape recorder and later transcribed on to data sheets for analyses. Territorial boundaries and individual home ranges were delineated by drawing a polygon around the cumulative routes followed by each individual. Estimates of group sizes were based on direct observation and the mark-recapture technique of labelled faecal stools as described by van Aarde & Skinner (1986).

Data on foraging behaviour of Clan B were analysed for 2 separate 'seasons' related to food abundance, December to May during and following pupping when an abundance of food was available and July to November when food, in the form of carcasses washed up, was much more scarce. Food diversity indices were calculated as suggested by Ebersole & Wilson (1980). All means are followed by one standard deviation of the mean and statistical significance considered at $P < 0{\cdot}01$.

Results

Range utilization

Direct observation and the capture-recapture technique described by van Aarde & Skinner (1986) showed that Clan A comprised nine individuals (five adults, four subadults), three of which were radio-collared. Clan B comprised three adult individuals, two of which were radio-collared. The entire home range of an adult male in Clan B fell within the home range of an adult female in that clan. The home range of an adult male and an adult female in Clan A similarly fell within the home range of an adult female in that clan (Fig. 1). It thus follows that the territorial boundaries of each of these clans coincided with the home-range boundaries of one of the individuals within the clan. The home range of Clan A included the town Luderitz, while Clan B concentrated on the seal colonies at Wolf and Atlas Bays. The territories of these clans overlapped by an area of $31{\cdot}7\,km^2$, representing 14·4% and 24·3% of those of Clan A and B, respectively. Individual home-range size varied from 31·9 to 220 km^2.

Rates of scent-marking were significantly ($F_{2,56} = 8{\cdot}99$) affected by the area of the home range that the individuals traversed, with rates while on patrol on the interior border of the home range ($\bar{x} = 3{\cdot}12 \pm 0{\cdot}44$; $n = 10$) being significantly ($t = 2{\cdot}45$) higher than when walking along the coast ($\bar{x} = 2{\cdot}18 \pm 1{\cdot}95$; $n = 30$), or in the interior parts of the range ($\bar{x} = 0{\cdot}81 \pm 0{\cdot}79$; $n = 19$). While on patrol these hyenas followed distinct routes which resulted in a network of trampled paths along which they scent-marked and where distinct latrines occurred.

Food availability

Carcasses were not evenly distributed along the coastline and the highest concentrations occurred between Wolf and Atlas Bay and at Grosse Bucht (Fig. 1). As a result of seasonal breeding and seasonality in the annual haulout pattern of these seals (*vide* Skinner & Smithers, 1990), the abundance of seal pup carcasses varied considerably throughout the year. Based on incidental counts of carcasses that washed up along a 1·5 km stretch of coastline between the seal colonies at Wolf and Atlas Bay, the calendar year can be divided into a period of food abundance (December to May) when the number of carcasses counted on a given day varied from 15 to 782 and a period of food scarcity (July to November) when the number of carcasses counted on a given day varied from 0 to 10.

Feeding behaviour

Members of both groups fed predominantly on carcasses of Cape fur seal pups (animals < one year old). Other food items taken included: black-backed jackals, domestic dogs, human refuse, and occasionally the carcasses of a variety of seabirds, springbok, fish, whales and an ostrich egg. Although carcasses were usually scavenged (Table I), seal pups were seen to be killed on eight occasions. The hyena would walk among the pups, bite a pup either on or behind the head, and then carry it out of the seal colony or away from the surf zone where it was usually partly consumed. Fresh carcasses were never completely consumed and hyenas usually ate the brain and intestines only. These hyenas occasionally darted after domestic dogs, flamingos or geckos in an attempt to kill them.

TABLE I

The frequency of occurrence of food items observed being eaten by brown hyenas living on the coast of the central Namib Desert. Values in square brackets are percentages of total and those in parentheses subtotals

Food item	Clan A	Clan B	Total
Arctocephalus pusillus	70	49	119[61·3]
Fresh carcass	(34)	(17)	51
Scavenged carcass	(34)	(26)	60
Kill	(2)	(6)	8
Canis mesomelas	–	6	6[3·1]
Canis familiaris	4	–	4[2·1]
Antidorcas marsupialis	–	1	1[0·5]
Unidentified bird	2	3	5[2·6]
Unidentified rodent	–	1	1[0·5]
Unidentified fish	1	–	1[0·5]
Unidentified scrap	33	1	34[17·5]
Other (unidentified)	8	1	9[4·6]
Human refuse	14	–	14[7·2]
Total	132	62	194

Clan A: Territory included Luderitz but no seal colonies
Clan B: Territory included seal colonies but not Luderitz

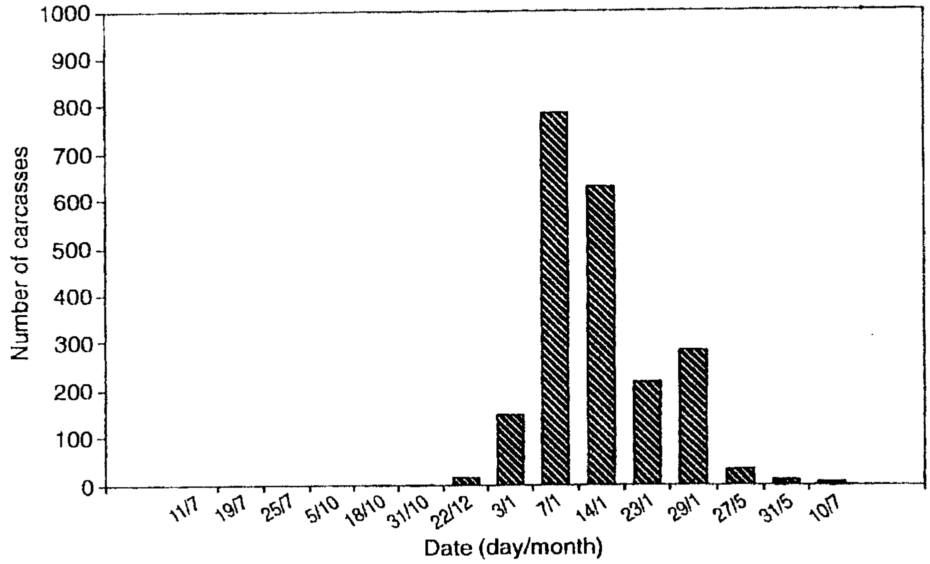

FIG. 2. The number of fur seal (*Arctocephalus pusillus*) carcasses counted along a 1·5 km stretch of coastline between Wolf and Atlas Bay on selected days between July 1982 and July 1983.

Food diversity index, calculated as suggested by Ebersole & Wilson (1980) for Clan A ($2{\cdot}78 \times 10^{-4}$) was nearly twice as high as that calculated for Clan B ($1{\cdot}57 \times 10^{-4}$). Members of Clan B obtained most of their food along 3·0 km of coastline in the immediate vicinity of the seal colonies, while members of Clan A obtained most of their food 4·5 km north of the seal colony along 6·0 km of the coastline (Fig. 1). A significantly ($\chi^2 = 12{\cdot}03$; $P < 0{\cdot}01$) higher proportion of food was located away from the coast by members of Clan A than by members of Clan B, and food items utilized by Clan A were more dispersed than those of Clan B (Fig. 1).

Individuals in both clans were predominantly active at night but even then spent a considerable amount of their time resting (Clan A = 46·8%, Clan B = 33%, Table II) but members of Clan B spent more of their time walking (58·4%) than those of Clan A (28%). These hyenas usually became active one to two hours after sunset and could remain active until sunrise or even later. On two occasions an individual was seen roaming within the seal colonies between 10:00 h and 11:00 h.

Information obtained on individuals in Clan B showed that the mean distance travelled per night, the time spent feeding, and the distance travelled until finding the first food item, were not affected by food availability. The distance travelled after feeding, however, did differ significantly ($t = 3{\cdot}64$; $d.f. = 35$) and the individuals spent more evenings on border patrol when food was relatively scarce compared to when food was relatively abundant (Table III).

Members of Clan A spent more time on feeding and food caching than members of Clan B (Table II). Members of Clan A also spent significantly more time feeding on fresh seal carcasses ($\bar{x} = 33{\cdot}5 \pm 16{\cdot}1$ min; $n = 32$) and scavenging old seal carcasses ($\bar{x} = 11{\cdot}0 \pm 8{\cdot}6$ min; $n = 34$) than members of Clan B ($\bar{x} = 19{\cdot}3 \pm 10{\cdot}9$ min; $n = 18$ and $\bar{x} = 5{\cdot}8 \pm 5{\cdot}5$ min; $n = 19$) ($t = 33{\cdot}57$ and $3{\cdot}62$, respectively: $P < 0{\cdot}01$).

TABLE II

Time (min) spent on various nocturnal activities by members of two clans of brown hyenas living along the coast of the central Namib Desert. Values in parentheses are percentages of the totals

	Time spent on activity (min)	
Activity	Clan A (N = 3)	Clan B (N = 2)
Walking/Foraging	12985 (40·34)	14761 (60·78)
Resting	15052 (46·76)	8069 (33·22)
Feeding	1860 (5·78)	574 (2·36)
Caching	749 (2·33)	214 (0·88)
Interacting	1332 (4·14)	430 (1·77)
Other	212 (0·66)	235 (0·97)
Total	32190	24283

Discussion

Earlier studies of resource utilization by brown hyenas in the Kalahari (Mills, 1990) and Magaliesberg (Skinner & van Aarde, 1987) have shown that territory size is determined by food availability. In the present study, this was not the case. Clan territories were large despite an over-abundant food supply concentrated along one margin of the territories where these hyenas found most of their food by beach combing. The larger clan occupied a larger territory than the smaller clan. With the former clan's food resource being more dispersed than that of the latter, it appears that under the prevailing conditions of abundance, dispersal of food has an influence on clan size and, as in the Kalahari (Mills, 1984), on territory size. This is also in agreement with the Resource Dispersion Hypothesis of Macdonald (1983) which suggests that territory size may be affected by the dispersal of available food.

Contrary to the Resource Dispersion Hypothesis (Macdonald, 1983), our observations suggest that, under the conditions prevailing in the study area, group size may be limited by the dispersal rather than the abundance of the food resources. On the other hand, this hypothesis does not preclude the possibility that animals may strive to maintain territories or groups that are larger than the minimum (Macdonald, 1983). All indices of intragroup aggression that have been recorded occurred in the vicinity of the seal colonies, and this implies that interference competition may limit food acquisition.

The territories of both clans stretched far beyond the dispersed food resources, but were smaller than the 330 km^2 for clans in the southern Kalahari (Mills, 1984), and of the same order as those in the central Kalahari (Owens & Owens, 1978). These intraspecific variations between different habitats may be explained in terms of variation imposed by food dispersion and quality. In the Namib, there were sufficient den sites near the coast, and pressure from intruders was unlikely as, with sparse food resources and huge distances to the next seal colony, other neighbouring clans appeared non-existent. Nevertheless, individuals scent-marked much more frequently when on border patrol than when walking along the coast. Avoidance of intruders might therefore be important. Intense border patrolling and scent-marking along selected routes suggests that the maintenance of territorial integrity is of importance to these neighbouring clans. Intergroup aggression was only recorded once, and it occurred within this area of territorial overlap.

It appears that food scarcity for a given part of the year has little influence on the feeding

TABLE III

The effects of food availability on foraging and feeding activities of members of Clan B. Values are given as mean ± one standard deviation of the mean. Values in parentheses present the number of complete nights (sunset to sunrise) the animals were radiotracked

Activity	Food abundant December–June	Food scarce July–November
Distance travelled per night (km)	12·9 ± 5·86(10)	19·85 ± 10·66(25)
Distance travelled for first food item (km)	8·22 ± 7·22(10)	7·53 ± 5·16(25)
Distance travelled after feeding (km)	3·97 ± 3·96(10)	12·7 ± 10·22(25)
Time spent feeding (min)	10·04 ± 10·69(26)*	11·44 ± 12·35(32)*
Percentage time active	59·96	57·31
Percentage time foraging	2·36	2·37
Number of nights on border patrol	3(17)	9(19)

* Values in parentheses include occasions when travelling distances could not be recorded.

behaviour of these hyenas. For the number of individuals in the clan, food was abundant at all times for scavenging and, as we observed, they were quite capable of killing pups if they needed to do so. Moreover, on analysis, the distance travelled to locate a food item was very similar in periods of food abundance and 'scarcity', as was time spent foraging, feeding and being active. On the other hand, distances travelled after feeding were much longer and more varied during food 'scarcity', as they spent 30% more time patrolling the interior and maintaining a territory. This may also be ascribed to searching for alternative food sources.

One would expect that it would be advantageous for these hyenas living under severe environmental conditions to minimize the area of their home range in order to minimize the costs of foraging and territorial defence. The intensity of scent-marking recorded for individuals patrolling the borders of their ranges suggests that territorial maintenance is of importance. The borders and ranges include ghost towns which are a relic from earlier diamond diggings; some of these having been inhabited 40–100 years ago by as many as 600 humans. They may well have provided relatively rich food patches, especially when considering that the seal colonies were then relatively small. It is thus just feasible that today's hyenas have 'acquired' their ranges from their predecessors. With resources at present being available in relative abundance and with relatively little time having been spent on food acquisition, these hyenas may well be able to afford to maintain the large territories they have 'inherited'. Carnivores are known sometimes to defend a larger area than the necessary minimum (Macdonald, 1983), but the advantages of this form of expansionism for brown hyenas is not clear. However, when considering the flexibility in the behaviour of carnivores, the maintenance of extended territories by these hyenas may serve to keep intruders well away from resource-rich areas on the coast.

Summary

The study is based on direct observation of two clans of brown hyenas living on the south-west coast of Africa in the Namib Desert. Although live prey in the form of seals in large colonies was available, the hyenas scavenged predominantly on seal (and seabird) carcasses washed up on the shore. However, seal pups were killed on occasion. Time spent foraging was not affected by carcass availability. Individual home-range size varied from 31·9 to 220 km^2 and food dispersal affected territory and group size. Although it would have been advantageous under the prevailing

environmental conditions to limit size of home range, this was not done. It is suggested that home-range size may result from acquired knowledge from previous generations of hyenas when conditions prevailing in the area were different.

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