

Resource dispersion, territory size and group size of black-backed jackals on a desert coast

Jan A. J. Nel, Rudi J. Loutit, Rod Braby, Michael J. Somers

Abstract We studied the relationship between resource—food patch—richness and dispersion on group and territory size of black-backed jackals *Canis mesomelas* in the Namib Desert. Along beaches where food patches are mostly small, widely separated jackal group sizes are small, and territories are narrow and extremely elongated. Where food patches are rich, fairly clumped and also heterogeneous, group sizes are large and territory sizes small. At a superabundant and highly clumped food source—a large seal rookery—group sizes are large, and territoriality is absent. Although jackals feed at the coast and den nearby, individuals move linearly far inland along well-defined footpaths. The marked climatic gradient from the cold coast inland—a drop in wind speed and rise in effective temperature T_e —and use of particular paths by different groups—strongly suggests that these movements are for thermoregulatory reasons only.

Keywords *Canis mesomelas* · Desert coast · Resource dispersion · Spatial organization

Introduction

Black-backed jackals *Canis mesomelas* are medium-sized (7–10 kg), opportunistic hunting and scavenging canids

which occur in a variety of habitats in south, east and north-east Africa (Loveridge and Nel 2004). They are nearly exclusively territorial, and conspecifics are actively excluded (Ewer 1977), but territory size differs markedly between habitats (Loveridge and Nel 2004). As data on food availability (richness and dispersion) in particular habitats are mostly lacking (Loveridge and Nel 2004), the effects thereof on group and territory sizes remain largely conjectural. Our study sites that differed markedly in food patch richness and dispersion allowed quantification of the influence of dispersed vs. clumped food resources on territory size and that of patch richness on group size of these coastal jackals. Jackals are resident on the Namib coast but virtually absent for up to 60 km inland, except intermittently along courses of ephemeral rivers. Territory boundaries here, as elsewhere, are demarcated through faecal and urine marking, often on prominent objects, and intruders vigorously expelled. However, as with golden jackals *Canis aureus* (Macdonald 1979), territoriality may be absent—i.e. territory advertisement and defence cease—where a superabundant (and conceivably indefensible) food source occurs (Nel 1984; Loveridge and Nel 2004).

Of all the habitats that the black-backed jackals occupy, the coastal Namib Desert of south-west of southern Africa is arguably the most hostile and challenging. On land, primary productivity is very low (Seely 1978), and potential food sources depauperate. Jackals on long stretches of coast are therefore highly dependent on allochthonous food input in the form of beached vertebrate carcasses (Nel and Loutit 1986; Avery et al. 1987; Nel et al. 1997). In addition, shelter, in the shape of coastal hummocks or widely-spaced dens, from the cold onshore winds is minimal on long stretches of beach, as well as on the salt flat or gravel plain hinterland.

Here, we compare food availability and black-backed jackal group size, density and territory (or home-range) size at three localities along the Namib Desert coast of Namibia. We also looked at food patch richness as well as dispersion

J. A. J. Nel (correspondence author)
Dept. of Botany and Zoology, University of Stellenbosch,
Stellenbosch 7602, South Africa
e-mail: jan@sun.ac.za

R. J. Loutit · R. Braby
Ministry of Wildlife and Tourism,
Windhoek, Namibia

M. J. Somers
Centre for Wildlife Management, University of Pretoria,
Pretoria 0002, South Africa

of patches. We counted jackals and estimated territory size at two of our three study sites. We quantify and stress the possible benefits of behavioural thermoregulation through escaping the low near-coastal effective temperature T_e (see also Skinner et al. 1984), even though food here is available nearly exclusively only on beaches.

Materials and methods

Study area

The Namib Desert of Namibia and southern Angola is hyperarid, with an unpredictable 8–15 mm p.a. rainfall at the coast (Lancaster et al. 1984). A pronounced climatic gradient prevails from the coast inland (Besler 1972; Lancaster et al. 1984; Skinner et al. 1984; Nel 1992). Onshore winds off the cold Benguela current can blow ≥ 6 h day⁻¹, from ca 0900 hours to late afternoon due to the inland desert being subject to strong isolational heating and convectionality by day (Logan 1960), and occasionally also into the night (Besler 1972; Lindsay and Tyson 1990), resulting in air drawn in from the adjacent cold (ca 10–12 °C) Benguela current. This results in low effective temperatures T_e , often below freezing, at the coast (Nel 1992). At night, insolation ceases, and the onshore wind dies down. Mean annual temperature along the coast is ca 15 °C (Skinner et al. 1984), with a daily amplitude of 5.9 °C (Besler 1972). Strong winds and low T_a by day can result in T_e below freezing. Free fresh water is available only in temporary pools after rivers flow, or from seepage to original deltas. High marine productivity results in varying numbers of fish, bird or mammal carcasses beaching along the coastline, as in other comparable situations (e.g. Polis and Hurd 1996, Rose and Polis 1998) and offering a food source for jackals.

The three localities along the coast of Namibia sampled were all located in conservation areas: (1) a ca 74-km stretch of beach, ca 40–45 m wide, in the Skeleton Coast National Park (hereafter SC) northwards from the Ugab River mouth (at 21°14' S, 13°36' E). Vegetated, low (<1–~3 m) coastal hummocks backing beaches occur sporadically (Dreyer and Nel 1990), but inland, on the flat gravel plains or salt flats, shelter is minimal. (2) Cape Cross Seal Reserve (CC) (21°45' S, 13°50' E), 120 km N of Swakopmund with, during our study, a ca 80–100,000 strong rookery of Cape fur seals *Arctocephalus pusillus* concentrated on a 4–6-km beach and a rocky cape. Coastal hummocks here are low (usually <1 m); vegetation is localised and sparse. Inland, low rocky hills afford some shelter. We sampled ca 6 km of beach (40–45 m wide) with its seal rookery, and an inland area of ca 8 km². (3) Sandwich Harbour (SH) (23°20' S, 14°25' E), a tidal lagoon, narrow salt–marsh complex and wetland ca 9 km long, between the barrier beach and high inland dunes,

is situated ca 50 km S of Walvis Bay in the Namib-Naukluft National Park. In contrast to the two other localities, wetland vegetation and depressions in the dune faces here offer abundant shelter from cold onshore winds. We sampled ca 3.5 km² of beach and adjacent wetlands and tidal flats at the northern end of the area.

Methods

Food availability and patch dispersion

Along the SC, beached bird carcasses were counted by RJJ and RB on 22 (total 898 km), mammal carcasses on 10 (466 km) and both on 12 (736 km) of the usual monthly beach patrols by vehicle and on foot. Particular patrols were one way, either N from the Ugab River mouth or S from different distances back, and varied from 6 to 74, $\bar{x} = 44.6$ km, preferably at or near low tide to allow driving on hard sand just behind the waterline. Carcasses (food patches) encountered were identified to species, and each carcass locality relative to the starting point of the particular patrol was recorded. Mean numbers of food patches (birds and mammals) per kilometre of beach were calculated for each count and year to reflect the dispersion of food patches. At CC visits by JAJN and assistants which lasted for 5–7 days, most observations on jackal groups—approaching or leaving the seal rookery, interacting and feeding—were made from parked vehicles for ca 5–8 h day⁻¹. Visits to SH by JAJN and assistants lasted 3–5 days. During 1983 and 1989, all carcass locations here were determined by searching the area on foot.

Mass of bird species recorded follows Maclean (1993). Mass of Cape cormorant *Phalacrocorax capensis* carcasses scavenged by jackals (as evidenced by tracks), compared to those of live birds ($n=20$ each), showed a mean of 53 % per bird consumed. This “utilisation” percentage subsequently was applied to all birds found scavenged. Beached birds could not be counted at CC itself as seals occupied the rocky cape and beach down to the waterline but were counted on the beach immediately to the north. Input (e.g. eggs, chicks, faeces and feathers) from four small breeding colonies (≥ 120 adults) of white-breasted cormorants *Phalacrocorax carbo* on shipwrecks and an abandoned oil rig on the SC, and palm trees at SH, was not quantified, although such input can be substantial (Polis and Hurd 1996). As beached fish carcasses were usually completely scavenged by jackals or Kelp gulls *Larus dominicanus* at low tide, their numbers and biomass could not be quantified.

Biomass of Cape fur seals available along the SC and at SH, and their dispersion, were derived from carcass counts, using a mean weight of 50 kg carcass⁻¹ (adult males, females and cubs combined (Shaughnessy 1981)), with an average of 52 % of a carcass consumed (sexes and all age groups combined; Panagis and Roberts, unpublished data).

We assumed a 5 % annual mortality of the ca 80,000–100,000 seals of all ages occurring at CC during 1982–1985, as recorded at seal rookeries further south along this coast (J.H.M. David, personal communication), and with 2.5 % of deaths occurring on land. However, as pup mortality at CC can be as high as 27 % (Panagis and Roberts, unpublished data), comparable to that of other *A. pusillus* rookeries on the Namibian Coast (De Villiers and Roux 1992; Oosthuizen et al. 1997), smaller carcasses are seasonally more numerous. Spacing of live seals or carcasses at CC could not be determined as entering the rookery was prohibited; however, seals belonging to particular harems tend to clump together. At SH positions of the few seal carcasses, found beached were plotted on a large-scale map of the area.

Mollusc density was quantified in 1-m² plots, at 5-m intervals, on 1-m wide transects ≥ 45 m long ($n=8$) across the beaches of the SC during 1984 and, with polychaete density as well, on 1-m² plots ($n=10$) on tidal flats at SH in 1989.

Rodent numbers and biomass on the SC were assessed in June 1989 by live-trapping on 0.25 ha of a vegetated area in the mouth of the Ugab River and on 1.2 ha of gravel plains ca 1 km N of the Ugab River mouth, and at SH on two 0.30 ha plots in vegetated hummocks and *Sporobolus* flats, respectively. These plots were all representative of the wider habitat available to rodents.

Density, group size and social organization of jackals

Jackal locations along beaches, group sizes, and any social interactions between groups were recorded by RJL and RB during 22 of 44 monthly beach patrols along SC, and on additional patrols during March 1982, March–April 1983, and November–December 1984 (six counts altogether) by JAJN and RJL, for a total of 2,515 km. At CC, group sizes and interactions between groups were recorded on 14 days altogether in March 1982 and 1983, May and August 1984, and May and June 1985, while linear densities were derived from three strip counts just inland of and along the entire seal rookery. At SH, JAJN recorded jackals' positions and group sizes—and thus density—and interactions, on 11 days altogether in March 1982, July 1983, June and July 1985, and June 1989 during foot patrols, and observations from high dunes backing the wetland by day and night.

Territory size

Jackal territory sizes along SC beaches were calculated by plotting positions of jackal groups or individuals encountered during patrols on maps of the census strips. Foot patrols helped determine northern and southern borders of beach use by particular groups; these borders were heavily faecal-marked on prominent features, e.g. whale vertebrae or shrubs, which can visually amplify territorial advertisement

(Hayward and Hayward 2010). Territory size was taken as beach length used \times average beach width. Localities of any agonistic interactions (fighting and flight by one group) between two groups were also plotted. At CC, short-distance movements of jackals and any interactions between individuals or groups were observed by day and night, mostly from parked vehicles, using 8 \times 42 binoculars. Size of home ranges here (no marking and territorial defence occurred, even though distinct landmarks, e.g. rocks, are present) are from Hiscocks and Perrin (1988), augmented by own records of jackal group movements. At SH, jackal groups were observed by day and on moonlit nights through binoculars from the high dunes backing the wetland; movements in the wetlands and vegetated areas were subsequently plotted on a map of the area, and territory size were determined from outer points and positions of faecal marking sites and groups' movements.

Temperature gradient from coast inland

Wet and dry bulb temperature and wind speed were measured 1 m above ground on the beach at Toscanini Bay, 50 km N of the Ugab River mouth (SC) and, from here, at 5-km intervals inland for 40 km along a transect at right angles to the coast, once during winter (July) and once during summer (December). Similar measurements were made along a transect inland from the beach just N of the seal colony at CC in winter (June). We used a Zeal wet- and dry bulb thermometer (G.H. Zeal Ltd., London) and a Munro anemometer (R.W. Munro Ltd., London). Effective temperature T_e (chill factor) was obtained from diagrams in Linacre and Hobbs (1977). Hill's cooling factor H (Lamb 1979) was calculated for each 5-km interval from the coast, using the equation

$H=(0.14+0.47V)(36.5-T)$, where V =median annual wind speed (in metres per second); T =mean annual air temperature (in degrees Celsius); and H =thousands of joules (in kilojoules per square centimetre of skin per second) lost (non-sweating condition). This cooling factor expresses the “cooling power” of air and thus the amount of “thermal comfort” experienced by an animal. Our data represent instantaneous and not mean annual readings. Additional information on longer term coastal climates were derived from the literature (e.g. Logan 1960; Lancaster et al. 1984; Skinner et al. 1984).

Results

Food patch richness

Bird and mammal carcass availability—richness and dispersion—differed markedly between the three sites over the study period (Table 1).

Table 1 Average availability of vertebrate food (kg km^{-1} coastline) at three sites on the Namib Desert Coast, Namibia, during 1982–1985

	Skeleton Coast ≥ 74 km coast sampled	Cape Cross ~ 6 km coast sampled	Sandwich Harbour ~ 3.5 km coast sampled
Food Availability			
Bird carcasses	$\bar{x} = 2.691$ (1.70–6.08) $n=34$	Not quantified (see text)	$\bar{x} = 8.35$, $n=2$
(at 53 % utilisation)	$\bar{x} = 1.426$ (0.903–3.22)		$\bar{x} = 4.25$, $n=2$
Mammal carcasses	$\bar{x} = 15.88$, $n=22$	$\bar{x} = 57.0$	$\bar{x} = 35.71$, $n=3$
Kg km^{-1} coastline	(7.69 – 207.14) $N=22$	(daily average) (see text)	
(at 52 % utilisation)	$\bar{x} = 8.25$ (3.97 – 107.71)	$\bar{x} = 29.2$	$\bar{x} = 18.56$
Total Bird+mammal for utilisation	9.68	> 29.2	22.81
Other			
rodents	2.04 kg ha^{-1} , $n=2$	Not sampled	1.77 kg ha^{-1} , $n=2$
fish/dogfish	See text	Not sampled	1.97 kg km^{-1} , $n=2$

Skeleton coast

Carcasses of 278 birds from 20 species (17 marine), and weighing from 50 to 5,500 g, were found beached. Cape cormorants (1,230 g) predominated (52.2 %). Of all carcasses located, 52 %, or 0.52 kg km^{-1} , were scavenged.

Neither numbers of beached birds (Kruskal–Wallis test, $\chi^2=2.292$; $df=3$, $P=0.514$) or mammals (Kruskal–Wallis test, $\chi^2=4.092$; $df=3$, $P=0.252$) varied significantly inter-annually (Table 2). Similarly, there were no significant differences in mass of beached birds between years (Kruskal–Wallis test, $\chi^2=3.250$; $df=3$, $P=0.355$), and also of mammals (Kruskal–Wallis test, $\chi^2=4.054$; $df=3$, $P=0.256$) (Table 2). Food patch richness therefore remained constant at this site. When available, eggs and chicks of ground nesting Damara terns (*Sterna balaenarum*) and White-fronted plovers (*Charadrius marginatus*) are heavily predated by jackal (Loutit and Braby, unpublished data), while jackals also caught live birds (especially Cape cormorants), often on take-off. Of 366 mammal carcasses beached, 362 (98.9 %) were Cape fur seals; four were Heaviside's dolphins *Cephalorhynchus heavisidii*. Only carcasses of adult seals beach along the SC, and can vary from $\bar{x} = 0.83$ (March–August, the fishing season), when seals can interfere with fishing operations and are occasionally shot, to $\bar{x} = 0.59$ (September–February, the closed season) carcasses km^{-1} of beach censused (Loutit, unpublished data). During our study, seal carcass availability varied both intra- and inter-annually, even during different patrols in the same month. The same applies to bird carcass availability.

Rodents were more numerous in vegetated patches at a river mouth than 4 km inland on gravel flats (4.05 vs. 0.02 kg ha^{-1}). In addition, colonies of Littledale's whistling rat *Parotomys littledalei*—potential jackal prey—inhabited coastal hummocks vegetated by low shrubs (*Salsola* sp.).

Mussels of four species had a mean density of 7.3 m^2 on eight transects of SC beaches. Density and biomass of the beach macrofaunal invertebrates at Toscanini Bay, about halfway along the study area, are given by Tarr et al. (1985). The 22 species they recorded totalled 8,774 m^{-1} with a biomass of 84 gm^{-1} . In addition, some nine coleopteran species, three dipterans, one amphipod and three isopods are associated with kelp wrack along beaches, and can be utilised by jackal (Tarr, personal communication).

Cape cross

Assuming a 2.5 % annual mortality on land of the 80,000–100,000 seals, and using a mean mass of 50 kg seal^{-1} , some 100,000–125,000 $\text{kg seal meat year}^{-1}$, or on average 274–343 kg day^{-1} , i.e. 45.7–57.2 kg km^{-1} in the rookery, would have been available, or, at a 52 % utilisation rate, 142–172 kg day^{-1} and 23.7–29.2 kg km^{-1} . Live seals as prey and dead seals on scavenge are present year round, and additionally, many placentas, stillborn pups, and those inadvertently killed by adults, are available during the pupping season (November–February). (De Villiers and Roux 1992; see also Oosthuizen et al. 1997). On beaches < 2 km north of the seal colony, bird carcass availability varied from 0 to 28 kg km^{-1} , or 0–34.44 kg km^{-1} ($n=2$). Although not quantified, birds were occasionally seen caught by the jackals. Mussel density was also not quantified but frequently seen gleaned from rocks (black mussels *Perna perna*) or dug up on the beach N of the seals colony.

Sandwich harbour

Two surveys yielded corresponding food availability (Table 3). Here, jackals also excavate polychaetes and eat plant matter (cucurbits *Acanthosicyos horridis* fruits). Live birds, including

Table 2 Bird and mammal carcasses available (mean±1SD) to black-backed jackal on the Skeleton Coast, Namibia, 1982–1985

Birds						
Year	Km counted	birds/count	N/km	Mass(kg) km ⁻¹	Mass available km ⁻¹ (53 % utilisation)	
	(no. of counts)	(range)	(range)	(range)	(range)	
1982	222 (8)	10.63±20.67 (1–65)	0.36±0.055 (0.03–1.63)	5.29±8.98 (0.25–27.16)	2.72±45.24 (0.13–13.71)	
1983	529 (12)	4.92±5.28 (0–19)	0.12±0.05 (0–0.38)	1.90±2.15 (0–5.37)	1.01±1.14 (0–3.04)	
1984	418 (8)	7.13±5.56 (2–21)	0.14±0.076 (0.04–0.28)	1.72±1.16 (0–3.74)	0.91±0.17 (0–1.98)	
1985	384 (9)	10.44±9.62 (0–34)	0.27±0.228 (0–1.82)	3.32±3.02 (0.33–2.24)	2.51±3.47 (0.08–11.85)	
=1,553 km						
Mammals						
Year	Km counted	N/count	N/km	Mass kgkm ⁻¹	At 52 % available	
1982	42 (1)	174 ^a	4.1	207 ^b	108	
1983	215 (4)	8.25±4.65 (4–14)	0.15±0.09 (0.07–0.26)	7.64±4.30 (3.70–12.96)	4.02±2.23 (1.92–6.89)	
1984	707 (15)	8.5±5.79 (2–19)	0.19±0.21 (0.04–0.36)	11.04±7.06 (2.03–35.0)	5.74±3.73 (1.06–9.45)	
1985	233 (3)	13.33±12.05 (5–31)	0.14±0.06 (0.07–0.42)	9.46±8.13 (3.38–20.95)	4.92±6.48 (1.76–10.89)	
=1,197 km						

^a170 cape fur seals *A. pusillus*, 4 Heaviside's dolphins *C. heavisidii*

^bMean mass of dolphins estimated at 50 kg

lesser flamingo *Phoenicopterus minor*, were regularly flushed from reed beds or bulrushes and caught, or cormorants, when taking off from the beach. Bird numbers, especially of Palearctic waders, fluctuate seasonally and annually, while those of inland water-birds and land-birds remain more constant (Loutit and Braby unpublished data). Previous counts (Berry and Berry 1975) showed monthly bird numbers to fluctuate between 3,000 and 14,000 birds.

Food patch dispersion

The spacing and number of carcasses km⁻¹ beach at SC (Table 2) shows food patch separation. Here, patches are far apart, whether they are bird (0.12–0.36 km⁻¹) or mammal (0.14–0.19 km⁻¹, or 4.1 km⁻¹ during the single count in 1982). Spacing between bird carcasses could vary between 0.1 and 10.1 km ($\bar{x} = 1.26$) over 38.3 km of beach censused, to 0.2–9.7 km ($\bar{x} = 4.18$ km) along 33.4 km of beach censused on different counts, with multiple carcasses occurring at some localities. At CC, the seal rookery seemingly presents an enormous, single food patch. Yet, due to the social structure of Cape Fur seals, this rookery is comprised of a large number of separate harems, with varying distances separating them.

Jackal group size and density

From 1982 to 1985, mean group sizes and density of jackals at the three localities differed significantly (Kruskal–Wallis test, $\chi^2 = 13.895$; $df = 2$, $P = 0.001$; and 17.407, $df = 2$, $P = < 0.001$, respectively) (Table 4). Along SC (overall mean = 1.77) and at CC (overall mean = 2.06), mean jackal group size varied significantly between years (Kruskal–Wallis test, $\chi^2 = 14.067$; $df = 3$, $P = 0.003$) and localities (Kruskal–Wallis test, $\chi^2 = 15.857$; $df = 3$, $P = 0.001$), respectively (Table 5). By contrast, mean group size at SH remained constant (Kruskal–Wallis test, $\chi^2 = 1.154$; $df = 2$, $P = 0.562$) at 2.25 during four years.

Short-term peaks in food abundance, e.g. mass stranding of birds and mammals, had no effect on either group size or density of jackal along the SC (mass of mammals vs. jackal numbers: $r = -0.112$, $P = 0.743$; mass of birds vs. jackal numbers: $r = 0.142$, $P = 0.676$; mass of mammals vs. jackal group size: $r = 0.505$, $P = 0.113$; and mass of birds vs. jackal group size: $r = 0.252$, $P = 0.454$).

Along both the SC and at CC, jackal density varied greatly (Table 4). At CC, jackal congregated at the northern (and densest) part of the seal rookery; here, aggregations of 16–32 ($\bar{x} = 24$, $n = 6$) jackals were found, resulting in high densities along ≤ 2 km of coast. At SH, densities varied less (Table 5).

Table 3 Mean food availability (kg km^{-1}) at Sandwich Harbour, Namib Desert coast, and at specified utilisation rates

Year	Fish	Bird	Mammal	Other
1983	0.66 ($n=1$) ¹ at 100 % utilisation rate	5.79 ($n=31$) ² 2.80 at 53 % utilisation rate Eggs and chicks ⁴	42.84 ($n=3$) 22.28 at 52 % utilisation rate	Rodents: ³ 2.2 kg ha^{-1} /1.25 kg ha^{-1} Fruits of cucurbit ⁵
1989	3.29 ($n=5$) ¹ at 100 % utilisation rate	10.9 ($n=31$) ⁶ 5.7 at 53 % utilisation rate Eggs+chicks ⁴	28,57 ($n=2$) 14,95 at 52 % utilisation rate	Mussels: ⁷ $\bar{x} = 2.8 \text{ m}^{-2}$; 100x1 m transect Polychaetes: 61.5±19.7 m^{-2} $n=11$ Fruits of cucurbit ⁵

n =number of carcasses or as indicated

¹ Bluntnose spiny dogfish *Squalus megalops*

² >50 % Cape cormorant *P. capensis*

³ Hairy-footed gerbils *Gerbillurus paeba*, probably totally consumed

⁴ From Grey Herons *Ardea c. cinerea* breeding in palm trees; number not quantified

⁵ "Nara" *Acanthosicyos horridis*

⁶ 86.6 % *P. capensis*; 5.9 % Kelp gull *L. dominicanus*; 1.18 % little egret *Egretta gazetta*; 1.97 % common tern *Sterna hirundo*; 3.5 % lesser flamingo *P. minor*; 0.79 % greater flamingo *P. rubber*

⁷ *Tapes corrugate* and *Leporimetis hankeyi*

Territory size

Along the SC, jackal groups usually were spaced far apart, occurring often at or near particular localities. The number of groups recorded varied between 1 and 5 per patrol, although seven groups occurred altogether. Spacing between group-frequented localities varied from 5 to 15.5 km, $\bar{x} = 10.5 \pm 1.17 \text{ km}$. Most inter-group interactions were agonistic, but occasionally seal carcasses were shared—successively fed upon by holders of adjacent territories. Although territories were extremely elongated— $\geq 15 \text{ km}$ of coastline—the narrow width ($\bar{x} = 45 \text{ m}$) of the beaches that contained food resulted in small overall territory size.

At CC, inter-group interactions were common, usually agonistic and mostly at seal carcasses on nearby beaches where up to 30 individuals from several groups congregated. Jackals were non-territorial with widely overlapping home ranges (a beach length of $\sim 6 \text{ km}$ and $\bar{x} = 25 \text{ km}^2$ (or 7.1 km^2 minimum area method)) (Hiscocks and Perrin 1988). As along the SC, feeding (on seal faeces, live seal pups, all seal and bird carcasses) were restricted to the beach habitat. Faecal marking, mostly on flat ground, but also on rocks, were common. At SH, groups were territorial and avoided each other. Territories were small ($\leq 1.2 \text{ km}^2$) and included parts of the beach and adjacent wetlands and were demarcated through urine and faecal marking, usually on vegetation. Tidal flats, when uncovered, were used by all groups; group activity (digging for mussels or tubeworms) by different groups being temporally spaced.

Temperature gradient

When jackals forage from late afternoon into the night, T_a drops only slightly, but winds cease, T_e correspondingly increases. By day, Hill's cooling factor H decreased markedly from the coast up to ca 40 km inland, as wind speed dropped and T_e conversely increased. $H > 20$ is regarded as extremely cold (see Lamb 1979).

As both ambient temperature and wind speed effect T_e and Hill's cooling factor H , moving inland where wind speed dropped and T_a increased would assist thermoregulation.

Jackal activity at the coast was little affected by T_a which fluctuated little over 24 h (Besler 1972), but noticeably so by T_e which dropped as wind speed increases from ca 0900–1700 hours. As wind speed increased by day, jackals sought shelter or moved inland at CC or the SC. During our observation periods, jackal at CC moved from inland to the seals during late afternoon when the wind dropped, and inland in the morning when wind speed increased and T_e dropped. During wind-free days, jackal remained near the seals, lying up on low hummocks or amongst boulders. This also happened intermittently during winter when hot east winds blow across the desert to the sea; coastal temperatures peak, and jackals now shelter as close to the cold sea as possible. At SH, jackals were active at all hours, but sheltered in thick vegetation when the wind came up, usually at 0900–1000 hours.

Table 4 Black-backed jackal group size, density (mean and range km⁻¹ beach) and social structure at three sites on the Namib Desert Coast, Namibia, during 1982–1985

n number of groups (size) or counts (density)

^aNorthern ≤2 km of seal rookery only

	Skeleton Coast	Cape Cross	Sandwich Harbour
Group size	1.51 (1–5) <i>n</i> = 164	2.01 (1–8) <i>n</i> = 538	2.32 (1–4) <i>n</i> = 22
Density	0.07 (0.04–0.1) <i>n</i> = 28	13.05 (7.11–16.3) <i>n</i> = 4	2.91 (2.0–4.0) <i>n</i> = 5
Social structure	0.06 (including blank counts) Territorial, but seal carcasses can be shared	32 (16–24) <i>N</i> = 6 ^a Overlapping home ranges	Territorial

Discussion

Acknowledging the limitations of our data in that our mean percentage utilisation rates, rates of pup mortality, and estimation of fish and invertebrate abundances are estimates based on a number of variable, some with assumptions, we believe our data overall show how jackals along the Namib Desert coast are heavily dependent on marine subsidies for food as are other canids in similar situations elsewhere, e.g. coyotes *Canis latrans* on the Baja California coast (Rose and Polis 1998). The situation on the Namib Desert coast is unique in that apart from open beaches and a seal rookery, a wetland is also present. These three habitats, although different and therefore difficult to compare, offers the opportunity of comparing the richness and dispersion of food patches, and their influence on a predator's group, territory or home range size, under a more diverse range of situations than anywhere else along desert coasts. In addition, the seemingly puzzling movements away from food-rich beaches far into the barren and food-deprived hinterland

can be explained by available data on changes in T_e from the coast inland.

Along the SC, carcasses beach unpredictably; however, jackals often beachcomb particular stretches, which could reflect local concentrations of beached prey. Spacing of these beachcombing areas would then account for differences in linear length of territories of different groups along the beach. As we argue below, linear inland movements of jackals along well-trodden paths, usually perpendicular to the coast here and at CC, are probably solely for thermo-regulatory reasons, and therefore should be disregarded when comparing the effects of food resources on territory size. At CC, jackal forage or hunt within or on the margin of a very rich, clumped and predictable food source—a seal rookery. In addition, they also forage or catch birds on beaches N and S of the rookery proper, but only a small part of beaches, rookery, or both, is used during a particular foraging bout. Their large overlapping home ranges at this locality reflect utilisation of shelter sites (rocky ridges, low dunes) by some jackals close to the seal rookery.

Table 5 Annual variation in group size and density (means ± 1 SD) of black-backed jackal at three sites along the Namib Desert coast, 1982–1986

Year	Group Size		
	Skeleton Coast	Cape Cross	Sandwich Harbour
1982	1.63 ± 0.99	2.8 ± 1.51	2.5 ± 1.5
1983	1.06 ± 0.25	2.01 ± 1.19	1.75 ± 0.86
1984	1.95 ± 0.80	1.87 ± 1.24	No data
1985	1.56 ± 0.78	1.75/2.35 ^a ± 0.88/1.04 ^a	2.5/2.80 ^a ± 0.71/0.80
1986	1.60 ± 0.97	No data	no data
1989	No data	No data	2.0 ± 0.89
Overall	\bar{x} = 1.57	\bar{x} = 2.19	\bar{x} = 2.32
	Density		
1982	No data	No data	2.86
1983	0.04/0.05 ^b	13.0	2.0
1984	0.04/0.09 ¹	No data	No data
1985	0.09	15.8/7.11 ²	2.86/4.0
1986	0.08	16.3	No data
1989	No data	No data	2.86
	\bar{x} = 0.07/0.09 ^b	\bar{x} = 13.05	\bar{x} = 2.91

^aCounts in different months

^bFirst figure includes blank counts; second ignores blank counts

Differences in resource richness and dispersion at our study sites, and concomitant differences in jackal spatial organization, are suggestive of the predictions of the resource dispersion hypothesis (RDH) (see Macdonald 1983). In addition, territory size (or length) and configuration seems to depend on the spatial dispersion of resources, usually ephemeral food patches (SC), or also long-term (rodents, cucurbits) (SH), which can be shared with minimal competition between group members. However, as our study sites differ markedly in configuration, our results cannot be directly measured against predictions of the RDH. The linear territories or home ranges can be equated to those of Cape clawless otters *Aonyx capensis* which are also linear, and which also appear to have their movements governed by distribution of high food density patches (Somers and Nel 2004).

The widely dispersed patches on the narrow Namib beaches (SC) result in very elongate but not necessarily large territories; the more clumped patches are (SH), the smaller the diameter of a territory, although these are larger in total area than along the SC if behind-beach inland movements are disregarded. However, due to constraints on behind-beach movements along the SC, inland borders of territories here could not be precisely established. Our results suggest that exposure to low T_e for long periods when foraging for long distances along narrow, linear beaches on the SC has the same, or larger, energetic drain on a jackal than when it forages in a smaller (diagonally) area; i.e. that length of exposure to energy-draining low T_e must also be considered a better measure of territory “size” than just surface area. In effect, the difference between Energy gain and Energy loss could therefore also influence territory size, rather than only patch dispersion. If so, the long exposure to low T_e by jackals foraging linearly along the SC therefore would equate with a “large” territory size. If we accept this caveat, then indeed wide-spaced food patches (SC) result in large territories, and clumped (SH) with small territories, as predicted by the RDH. At CC, seal rookery subsets of the enormous food source—individual seal carcasses or live pups—are difficult to defend, due to seal movements and those of other jackals within the rookery, and makes territorial defence impossible; overlapping home ranges result. These include some shelter close to the seal rookery.

Jackal group sizes along the SC are small, large at CC and large at SH. Here, difficulties of dispersal for young jackals (the inland sand sea, other resident groups north and south of SH) could inflate group size. But at both CC and SH, the larger groups could reflect the prediction of the RDH that group size reflects food patch richness and not territory size. The somewhat smaller mean group size at CC, in comparison to SH, could be an artefact of sampling; jackal groups approaching the seal rookery tend to spread out, making determination of group size difficult at times. In addition, the enormous and inexhaustible food source could

also hasten dispersion of cubs, leading to the smaller groups during our study period. At both SC and CC, “helpers” are present at dens with cubs (Loutit and Braby, unpublished data) but the situation at SH is unclear.

On long stretches of coast, shelter on or behind beaches is sparse, and jackals move far inland into the unproductive hinterland; this also occurs at CC even though more shelter near the sea (seal colony) is available. Given the mostly low T_e at the coast and sharp rise inland, the most parsimonious explanation for such movements is that they are for thermoregulatory reasons; where adequate shelter just behind the beaches is available, as in wetlands at SH, inland movements are virtually absent.

The energy expended on thermoregulation could be substantial and offset losses due to inland movements. Our data point to the thermoregulatory benefits (and by extension, reduced food requirements) afforded by escaping from the harsh coastal environment. Data on the climatic gradient from the coast inland help explain the otherwise puzzling phenomenon of jackals moving away from the resource-rich coast into the barren hinterland; they do so to escape the energy-sapping low effective temperatures.

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